PREDICTING LODGING IN WINTER WHEAT

by

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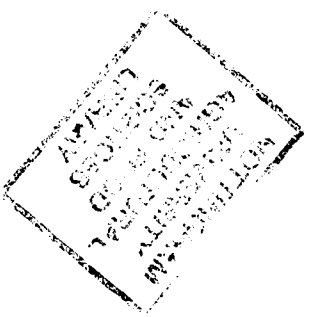
BSc Hons.



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ABSTRACT

Lodging, the permanent displacement of plant stems from the vertical, occurs on average once every four years in UK wheat crops, when it reduces the yield and bread making quality of grain. Lodging usually occurs in the summer and control is most commonly sought by applying growth retarding chemicals in the spring. This thesis develops a method of predicting which crops are prone to lodging so that spring lodging controls can be targeted most effectively.

A model was developed in association with this study which calculates stem and root lodging risk from summer-time plant, weather and soil factors. The spread of the plant's root plate, the stem diameter and the number of shoots per plant were shown to have very strong influences on lodging. Structural rooting depth, stem failure yield stress, height at centre of gravity and the rate at which stems oscillate in wind (natural frequency) were also important, but less influential.

Methods of predicting the most important lodging-associated plant characters from crop observations in spring were developed from the literature. These were then tested through experiments in 1995 and 1996 with factorial combinations of crops sown in late September and late October, at 500 seeds m^{-2} and 250 seeds m^{-2} and with large and small levels of residual soil nitrogen. Early sowing, dense seed rates and fertile soils all increased stem and root lodging, with sowing date having the greatest influence. Plants sown at high densities had small root plates and were poorly anchored; they also had fewer shoots causing a smaller leverage. Early sown plants had shoots with a high centre of gravity and slow natural frequency, causing a greater leverage. Plants sown early on fertile soils had narrow, weak stems.

Final shoot number per plant was predicted with good precision (R^2=0.94) from spring plant number m^{-2} and maximum shoot number m^{-2} using a model of tiller survival. Stem diameter was predicted with moderate precision (R^2=0.57) from spring canopy size and shoot number m^{-2}, via a calculation of the amount of dry matter partitioned to each stem base. Root plate spread showed a linear and inverse

relationship to spring plant density (R^2=0.48), mainly as a result of variation in the length of the rigid roots and in the width of the plant base.

It is concluded that early season crop observations have the potential to predict the values of the most influential lodging-associated plant characters, from which a model of lodging can calculate the proneness of crops to stem or root lodging in time for remedial action. The next steps would be to develop prediction schemes for other plant characters which influence lodging and test all the predictions in a wider range of crops, sites and seasons.

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GENERAL ABBREVIATIONS

kg = kilograms

g = grams

t = tonnes

l = litres

ha = hectares

Hz = hertz

Nm = Newton metre

Nmm = Newton millimetre

mm = millimetre

cm = centimetre

m = metre

s = second

GAI = green area index

N = nitrogen

DM = dry matter

OM = organic matter

GS = plant growth stage (Zadok's)

PGR = plant growth regulator

HI = harvest index

TGW = thousand grain weight

SPWT = specific weight

cv. = cultivar

LTM = long term mean

ADAS = Agricultural Development and Advisory Service

MAFF = Ministry of Agriculture, Fisheries and Food

NIAB = National Institute of Agricultural Botany

Site codes

MT95 = main husbandry experiment in the 1994-95 season.

VT95 = variety experiment in the 1994-95 season.

MT96 = main husbandry experiment in the 1995-96 season.

1. INTRODUCTION

1.1 THE HGCA 'LODGING PROJECT'

Lodging is the permanent displacement of plant stems from the vertical (Pinthus, 1973) which frequently causes serious yield losses in UK grown cereals. To help maximise the profitability of UK cereal production the understanding and prediction of lodging must be improved. The lodging mechanism and factors which influence lodging have been comprehensively reviewed by Mulder (1954) and Pinthus (1973) and further investigated by Graham (1983), Easson *et al.*, (1993) and Crook and Ennos (1993). Despite this work much conjecture still exists about how best to prevent lodging and guidelines for reducing lodging are based on intuition rather than comprehension.

It is the aim of the Home Grown Cereals Authority (HGCA) funded 'Lodging Project' to test the belief that crop inspections in the spring, together with other intelligence can be used to significantly improve a) the assessment of lodging risk, and b) the identification of effective controls.

To help achieve these aims an array of experimental treatments were used to investigate the elements of husbandry known to be critical in determining lodging risk, together with remedial controls thought most likely to reduce lodging. These investigations have been closely associated with the first mechanistic model of lodging, which was originally outlined by Baker (1995) and has been further developed by Baker *et al.*[1] (Appendix 1) and by Griffin (1998). Griffin (1998) used the lodging model with crop measurements from the 1994-95 husbandry experiment described in this thesis to further understand the mechanism of lodging and elucidate the influence of environmental and husbandry factors on the process.

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1 'A method for assessment of the risk of lodging in wheat'. The Journal of Theoretical Biology, *In press*, see Appendix 1.

The main aim of this thesis was to continue the work within the overall 'Lodging Project' by developing methods to predict the summer-time state of a winter wheat crop from spring observations. If such prediction schemes could be shown to operate successfully, they could be used in conjunction with the lodging model described in Baker *et al.* (Appendix 1) for the early season prediction of lodging risk, in time for remedial controls to be administered.

The term 'lodging risk' is central to this study and requires a clear definition. 'Risk' is the uncertainty of a particular outcome and is used in two senses in this thesis. The first type of 'lodging risk' describes the uncertainty of lodging given information about the crop, but not the weather, at the time of lodging. This type of risk is 'calculated' by the lodging model of Baker *et al.* (Appendix 1). The second type, which is used more commonly, describes the uncertainty of lodging using information about the crop from its pre-lodging period e.g. the spring. This type of risk includes an additional element of uncertainty associated with 'prediction' in time. It is often used in conjunction with early season husbandry decisions such as varietal choice, nitrogen applications and plant growth regulator (PGR) applications.

This chapter explains how lodging reduces profit margins and examines how lodging is perceived and understood by farmers and agronomists. Furthermore, environmental and plant factors which are believed to influence lodging risk are introduced from a brief examination of the relevant literature. Methods of minimising lodging are analysed and the importance of predicting lodging risk in time for remedial action is explained. Finally, the lodging model of Baker (1995) and Baker *et al.* (Appendix 1) is briefly introduced, the specific aims of the thesis are described and the thesis content outlined.

1.2 THE COST OF LODGING TO THE FARMING INDUSTRY

When lodging occurs the profitability of a cereal crop can be drastically reduced through decreased yield. This may be caused directly by reduced dry matter accumulation or indirectly because of incomplete recovery of the crop at harvest. Profit margins are further reduced by increased combining time, grain drying costs and reduced grain quality especially through low Hagberg falling numbers. Quality is particularly affected if harvest is delayed and the grain sprouts. Widespread lodging occurs on average once every four years and is often associated with wet summers. The summers of 1980, '85, '87, '92 and '97 are generally regarded as seasons with serious lodging in recent years.

Yield losses of between 0 and 45% have been observed in artificially lodged experiments (Weibel and Pendleton, 1964; Laude and Pauli,1956; Mulder, 1954; Stapper and Fischer, 1990). The level of yield loss depends on the severity of lodging and the growth stage at which it occurs. The largest yield losses are associated with lodging which occurs soon after anthesis, especially during grain filling, thereafter yield losses decline (Weibel and Pendeleton, 1964; Fischer and Stapper, 1987). During the severe lodging in 1992, when 16% of the UK wheat crop lodged (Berry *et al.*, 1998), yield losses of 0 to 45% would have cost growers up to £130 million, based on 1992-93 average prices of feed wheat (HGCA, 1993). Lodging in 1992 also caused a reduction in grain quality, with Hagberg falling numbers decreasing from a five year UK average of 287 to 254 and thousand grain weight decreasing from 45 g to 39 g (HGCA, 1993). This resulted in a smaller quantity of the wheat crop reaching milling quality, thereby reducing growers income further through the loss of milling premium, which usually varies between £15 and £25 (HGCA, 1993).

The cost of controlling lodging is also high and the application of PGRs often occurs regardless of lodging risk as an 'insurance measure'. For example in 1996, when there was moderate lodging, PGRs were applied to 79% of the UK wheat area at a cost of 10.6 million pounds (Garthwaite *et al.*, 1996), and in 1994 when lodging was not widespread, 74% of the UK wheat area was treated (Garthwaite *et al.*, 1994). In

years of widespread lodging the application of PGRs clearly has not prevented lodging (Woolley, 1992). Hence there is a need to understand more fully how lodging risk is influenced to enable control measures to be targeted more effectively.

1.3 GROWERS' PERCEPTION OF LODGING

Two common types of lodging have been identified, stem lodging and root lodging. Stem lodging results from the bending or breaking of the lower culm internodes, whilst root lodging is due to failure of root anchorage and results in straight, unbroken culms leaning from the crown. To date few studies have been carried out which define the causes of lodging and much information about lodging is reliant on observations made by growers. It is generally agreed that lodging is due to an interaction of the plant with the environmental factors rain, wind and soil. The majority of growers perceive stem lodging to be the most common form of lodging. However, debate ensues among scientists as to whether stem lodging or root lodging predominates. Studies by Pinthus (1973), Graham (1983), Ennos (1991) and Easson *et al.*, (1993) favour root lodging, although studies by Neenan & Spencer-Smith (1985) suggest that stem lodging is more likely. It would appear that both types of lodging are important, although scientists have recently regarded root lodging as more common, especially following the introduction in the late 1970s of dwarf varieties with shorter and stronger stems.

It is clear that the weather plays an important part in determining lodging risk. Rain increases lodging risk by decreasing soil strength and increasing the load which the plant base must bear. Wind then acts as the force which pushes the plant over or buckles the stem. However, despite its importance very little has been published which quantifies the weather conditions necessary to cause a lodging event. Easson *et al.* (1993) observed that lodging occurred gradually over a period of 24 hours during which rain fell and could occur with low wind speeds. Lodging was also found to be more closely associated with the occurrence of rainfall than the amount of rainfall. Our analysis of meteorological records over the last 15 years (unpublished) has shown

that the lodging years of 1980, 85, 87 and 92 experienced a wetter than average July with a higher than normal frequency of rain days.

It is well known that lodging risk is strongly influenced by a number of husbandry decisions including variety choice, sowing date, seed rate, drilling depth, the rate of nitrogen application and the application of PGRs (Sylvester-Bradley and Scott, 1990; Pinthus, 1973). It is envisaged that their influence on lodging risk is through their ability to alter crop structure by affecting certain plant characters. Varietal differences in lodging risk are summarised by standing power scores (NIAB, 1996), but are believed to be due to a number of different plant attributes. Good relationships have been observed between the lodging resistance of different varieties and plant height (Sylvester-Bradley and Scott, 1990), earliness of maturity (Fischer and Stapper, 1990), stem diameter and wall width (Pinthus, 1973) and root plate spread and root strength (Crook and Ennos, 1994). Early sowing may increase lodging risk through its effect of increasing plant height (Fielder, 1988), increased final biomass (Green and Ivins, 1985) and higher maximum and final shoot number per metre squared (Green *et al.*, 1985). High seed rate may increase stem lodging risk by reducing the diameter of basal internodes (Easson *et al.*, 1993), or it may increase root lodging risk by reducing the number of supporting roots per stem (Easson *et al.*, 1993) and reducing root strength (Easson *et al.*, 1995). If drilling depth is less than normal crown depth, lodging risk may be increased through shallower anchorage. High rates of nitrogen applied early may increase lodging risk by increasing height at centre of gravity through greater stem height and canopy weight, by decreasing stem bending moment and by decreasing crown root bending moment and number (Crook and Ennos, 1995). Plant growth regulators may reduce lodging risk by more than one method (Crook and Ennos, 1995). Plant growth regulators applied during stem extension (GS 30 to GS 45) reduce plant height. This lessens the moment that the aerial part of the plant imposes on its base thereby reducing lodging risk. There is also a common perception that PGRs applied at early stem extension strengthen the lower internodes, thereby reducing the risk of stem lodging. Finally, some PGR manufacturers claim that PGR

application during the tillering phase improves plant anchorage. However, scientific evidence to support this is difficult to find.

1.4 MINIMISING LODGING

It may be suggested that lodging risk will usually be minimised by careful consideration of early husbandry decisions such as varietal choice, sowing date, seed rate and nitrogen application. In practice this is often not the case, as the search for greater profit margins means that 'high lodging risk' husbandry decisions are often taken. Many high yielding or bread making wheat varieties have high lodging risk characteristics such as tall and weak straw. Early sowing is common because high yield potential is linked with earliness of sowing (Fischer and Stapper, 1990). Large seed rates are often used to avoid the potential risk of low yields due to poor plant establishment. Greater than necessary nitrogen applications are often made due to poor estimation of soil mineral nitrogen and imprecise nitrogen recommendations (Sylvester-Bradley, 1996). Any one of these factors, or a combination, can result in the production of winter wheat with a large perceived lodging risk. As many of the husbandry decisions which influence lodging risk have been taken by this stage, the problem of how to reduce lodging risk arises. This is most commonly achieved by applying PGRs between the stages of tillering and flag leaf emergence. Reducing spring nitrogen applications or occasionally rolling before the beginning of stem extension are also employed. Spring intervention can be expensive; plant growth regulators cost between £5 and £33 ha $^{-1}$, whilst reducing nitrogen can reduce yield (Sylvester-Bradley, 1993). Hence, the control of lodging presents a significant and challenging problem; it usually occurs in the summer, but its risk can often only be minimised by intervention in the spring. Therefore, unless all crops are treated with lodging controls, a method of predicting lodging risk in the spring is required, which will identify crops with the least risk. This will allow appropriate remedial action to be targeted only at crops with a high lodging risk.

As already described, lodging risk is determined to some extent by uncontrollable weather conditions during the lodging risk period and the soil type. However, it is also evident that lodging risk can be influenced by decisions such as varietal choice, sowing date, seed rate, nitrogen rate and the application of PGRs, through their effect on crop structure. These findings suggest that at the time of lodging the state of the crop is important in determining lodging risk. Thus, early season crop observations may prove useful indicators of lodging risk, and could form the basis of a prediction scheme of lodging risk.

1.5 MODELLING LODGING

From a grower's view point lodging is influenced by the weather conditions at the time of lodging together with a large number of plant characters. It appears to be the complexity of the lodging process that explains the poor understanding of its control. Nonetheless, the propensity for a plant to lodge could be seen to be influenced by just three distinct plant components; the moment which the aerial part of the plant imposes on its base, its stem base failure moment and its root anchorage failure moment. To help simplify and understand the lodging process mechanistic models have been developed for each of these three plant components (Crook and Ennos, 1993; Baker, 1995). These models have been combined to produce a comprehensive model of the lodging process (Baker *et al.* (Appendix 1)) which, when further developed, could act as a useful method to analyse the causes and predict the risk of lodging.

1.5.1 Aerial component of the model

To model the moment which the aerial part of a wheat shoot imposes on its base, a scheme originally used for evaluating the windthrow of trees has been suitably modified by Baker (1995). The basic model assumes that a shoot of a wheat plant can be represented by a lumped mass at the top and bottom of a weightless, but elastic stem, under the action of a horizontal wind force and its own mass. Along with wind speed, requirements for calculation of the aerial force of a shoot are the natural frequency of its stem and its height at centre of gravity. Other requirements for this

calculation, including the ear area, drag coefficient and damping ratio, were estimated from published data (Baker, 1995). The natural frequency is the frequency of oscillation of free vibrations of the stem in response to a deflection caused by a wind gust. Natural frequency acts as the basic controlling parameter of the aerial model and draws together a number of factors which affect the plant's aerial force including height at centre of gravity, ear weight and stem stiffness (Baker, 1995). Wind speed values required by this model are estimated from long-term weather data as described in section 1.5.4. Most plants have more than one shoot, therefore to calculate the aerial moment of the whole plant it is necessary to multiply the aerial moment, calculated for one shoot, by the total number of shoots per plant. It must be noted that this method ignores any differences between shoots.

1.5.2 Stem base component of the model

Stem base failure moment can be calculated from basic structural theory (Baker, 1995), using the material strength of the stem wall (failure yield stress), the external stem diameter and the stem wall thickness. It should be noted that failure is assumed to occur due to tensile stresses in the stem exceeding the failure yield stress. This is unlike the approach adopted by Graham (1983) and Easson *et al.* (1992) who assumed that failure occurs due to stem buckling in compression. This different approach resulted from comparing the same stem strength values for stem failure in both tension and compression. In all cases, values for tensile stem failure were substantially lower than values for compressive stem failure, indicating that failure in tension is likely to be the primary failure mechanism of the stem, even though the stem may subsequently be seen to buckle.

1.5.3 Root anchorage component of the model

Root anchorage failure moment has been modified from the method of Crook and Ennos (1993) and uses values of the spread of the structural roots, soil shear strength and a constant. This constant is a function of soil type, soil water content and crown root structure, and has been calculated theoretically by Crook and Ennos (1993) to be 3.5. However, by mechanically loading plants our own experiments suggest a much

lower value of 0.4 (Griffin, 1998). Soil shear strength is calculated for the depth of soil to which the structural roots extend using the method described in Baker *et al.* (Appendix 1). This calculation requires values of the daily rainfall, soil water content at permanent wilting point and saturation point, clay content, the ADAS visual score for soil structure (MAFF, 1982), and structural rooting depth. The soil water content at permanent wilting point and saturation point and clay content can be estimated from the soil type, whilst soil visual score and structural rooting depth can be measured in the field. Daily rainfall is predicted from long-term weather data of a particular site, as described in section 1.5.4. Soil shear strength decreases for a greater water content, greater visual score for soil structure and smaller clay content.

1.5.4 How the lodging model works when the three components are combined

To simulate field conditions the model depends on the environmental characteristics of the site, including long-term wind and rain data and soil type. From these data probability distributions for the daily maximum hourly mean wind speed and daily rainfall are calculated. From these distributions a Monte Carlo simulation technique is used to generate a 1000 random values for the hourly mean wind speed and the average daily rainfall. The shear strength and soil saturation (wetness) of the soil, along with the plant natural frequencies are then calculated for each data set. The bending moment imposed by the aerial part of the plant in the simulated wind conditions is then estimated, using the method of Baker (1995). Simple principles of structural analysis and the root anchorage model based on Crook and Ennos (1993) are then used to calculate the stem failure moment and the anchorage failure moment respectively. The likelihood of stem and root lodging can then be ascertained by comparing the three moments. Stem lodging is predicted when the moment imposed on the stem base by the aerial part of a shoot is greater than the stem base failure moment. Root lodging is predicted when the moment imposed on the plant base by the aerial parts of all the shoots of a single plant is greater than the anchorage failure moment. The 'lodging risk' predicted by the model is the probability of lodging occurring at a particular site during any one lodging period (40 days centred on July). For example if a 0.5 probability is given as the predicted 'lodging risk', then for

typical wind and rain distributions of a particular site and time period, lodging would be expected once every two years.

1.6 THESIS AIMS

It has been shown that lodging is influenced not only by uncontrollable weather conditions, but also by the state of the crop during the lodging risk period. The state of the crop can be affected throughout its growth by earlier husbandry decisions such as varietal choice, sowing date, seed rate and nitrogen supply. This suggests that early season crop observations may provide early indicators of lodging risk at the stage of plant development when effective remedial action can be administered.

The challenge of predicting lodging in winter wheat has been approached by attempting to develop schemes to predict the summer-time values of the plant characters associated with lodging identified by Baker (1995) and Baker *et al.* (Appendix 1). These prediction schemes are expected to be based upon early spring plant measurements and field observations, and then rely on an understanding of the development and growth of the plant character in question through the rest of the growing season. It is envisaged that such prediction schemes might be used in conjunction with the lodging model to provide a quantitative prediction of the summer-time lodging risk in time to influence decisions about remedial action in the spring.

The overall aim of this thesis is to;

- **test the hypothesis that spring crop observations may provide early indicators of lodging risk**

This will be achieved by;

- developing and testing schemes which predict the summer-time values of plant characters associated with lodging, using spring plant measurements and field observations.

- understanding how the lodging-associated plant characters develop and grow in different seasons and for different varieties and husbandry practices, which will help develop the prediction schemes.

1.7 THESIS STRUCTURE

Chapter 2 reviews the literature concerning the plant characters required by the lodging model, which were introduced in this chapter. The plant characters are considered depending on whether they influence (i) the stem base component, (ii) the aerial component or (iii) the root anchorage component. An account of growth and development is given for each plant character followed by the influence of environmental, varietal and husbandry factors. This chapter ends with a recap of the challenge and a justification of the experiments used to meet this challenge.

Chapter 3 describes the materials and methods used in the experiments. Chapter 4 describes the general crop growth throughout the season in the lodging experiments and relates this to the lodging observed. Chapter 5 reports development and growth of each lodging-associated plant character, and how this is influenced by season, variety and husbandry. This chapter concludes by ranking the importance of each plant character in terms of predicting lodging risk. In Chapters 6, 7 and 8 prediction

schemes linking crop measurements at the beginning of stem extension (GS 30) with summer-time values of the lodging-associated plant characters are set up and either tested or developed further. Chapter 9 discusses the findings of the thesis and puts them in context with the broader aims of the HGCA funded 'Lodging Project' and growers' requirements.

2. LITERATURE REVIEW

2.1 BACKGROUND

A mechanistic model for the calculation of lodging risk has been described briefly in Chapter 1 and is described in full detail in Appendix 1. This model requires inputs of the summer-time values of a number of plant characters associated with lodging, together with weather and soil information. To be useful to the grower the summer-time lodging risk must be predicted in the spring, in time for remedial intervention. Therefore, predictions of the summer-time values of these important plant characters are required, based on crop observations taken earlier in the season. Development of these prediction schemes depends upon an understanding of the growth and development, and the influences of site, season, variety and husbandry for each lodging-associated plant character. These plant characters encompass roots, tillers, stems and ears, so an understanding is required of the growth and development of the whole plant from sowing to maturity. To achieve such a task, a degree of assumed knowledge must be expected, much of which can be found in the crop physiology text books and reviews by Evans (1993), Hay and Walker (1989), Gallagher (1984), Austin and Jones (1974) and Sylvester-Bradley and Scott (1990).

The understanding central to this thesis concerns the way the wheat plant grows and develops throughout its life cycle. Therefore precise definitions of growth and development are essential. From sowing through to harvest the wheat plant passes through a sequence of well-defined developmental stages that lead to the production of leaves, tillers and floral structures concurrent with an increase in crop weight. Two distinct physiological processes progress concurrently to account for these changes during the life cycle of the wheat plant; **growth** and **development**. Growth refers to an increase in crop size or weight, whilst development refers to the changes in plant form, e.g. onset of tillering and stem extension, that occur from the seedling to the mature plant at harvest. Both processes are affected by environmental conditions and husbandry. The rate of crop growth is directly related to the amount of radiation intercepted by green tissues (Biscoe and Gallagher, 1977). Any factors

which affect the expansion and persistence of the green leaf area, such as nutrient supply and disease, will affect growth. The rate of crop development is dictated by temperature and the seasonal cycle of day lengths. The rates of growth and development are not always correlated e.g. bright, cool conditions will result in fast growth rates and slow developmental rates, whereas dull, warm conditions will result in slow growth rates and fast developmental rates. Also, slow development due to cool conditions, although accompanied by slower growth, indirectly leads to more growth per unit of development because development tends to be prolonged more than growth is decreased. Therefore, the size of different components of the wheat plant depends on the balance between growth and development during the phase when the particular component is being determined e.g. large numbers of tillers per plant will result when a high growth rate and prolonged development occur during the phase of tillering.

The growth and development of the plant characters associated with lodging will be dealt with in the order according to the model component they influence. The stem base component will be dealt with first followed by the aerial and the root anchorage components. This order has been chosen because information about some of the plant characters in the stem component is needed to understand the development of the plant characters in the aerial component. Likewise, some of the anchorage component plant characters are reliant on those in the aerial component. The aerial component has been divided into two parts. Firstly, the part required to calculate the moment imposed on the stem base by one shoot. This is used with the stem base failure moment to calculate the stem lodging risk. Secondly, the part required to calculate the moment imposed on the plant base by all the plant's shoots. This is used with anchorage failure moment to calculate the root lodging risk. Within each of these model components plant characters are often closely related and usually develop concurrently. Therefore these similar plant characters are considered together. Using this order, each plant character is first defined followed by a description of its growth and development in different environmental conditions. Finally, the influences of varietal and husbandry decisions on each plant character are considered.

2.2 THE STEM BASE COMPONENT OF THE MODEL

The elongated stem consists of a series of jointed, often hollow internodes connected by solid swollen meristematic nodes. Stem morphology varies along the stem base e.g. stem diameter increases from the most basal extended internode to the third extended internode (Easson *et al.*, 1993). To help account for this variation stem base components of the model refer to measurements at the mid point of the most basal extended internode greater than ten millimetres in length. Stem base failure moment is determined by the geometrical and material properties of the stem, and can be calculated from basic structural theory (Baker, 1995). This calculation uses the geometrical properties of stem diameter and stem wall thickness, with the material property stem failure yield stress.

Stem diameter and wall width are closely related to stem dry weight per unit length and lodging resistance (Atkins, 1938; Mulder, 1954; Pinthus, 1973; Austin and Jones, 1977). For this reason stem dry weight per unit length is sometimes used as a substitute when specific data concerning stem diameter and wall width is not available. It will be shown that the stem diameter and stem wall thickness develop concurrently and will therefore be considered together.

The failure yield stress of the stem wall is the load applied to a structure per unit cross sectional area to cause it to fail, and is the product of Young's modulus of elasticity and the strain at failure. Young's modulus of elasticity is the ratio of stretching force per unit cross sectional area to the elongation per unit length. This measurement is independent of the geometric properties of a structure and is entirely dependent on the bonds between the molecules of which the material is composed. This measurement is sometimes described as 'stem stiffness'. Strain is the proportion of the original dimensions by which the structure deforms. Lodging resistance has been linked with a number of material properties of the stem, including vascular bundle number, width of the sclerenchyma layer and the proportions of lignin, cellulose and hemicellulose

present in the cell wall, (Pinthus, 1973). Lignification occurs predominantly in the vascular, sclerenchyma and parenchyma tissues, which may explain why the number of vascular bundles and sclerenchyma width have been associated with lodging resistance. Stem failure yield stress continues to develop after stem diameter and stem wall width have finished developing, and is considered separately.

2.2.1 Growth and development of stem base

Stem growth begins shortly after floral initiation when the plant enters its reproductive stage and ends soon after anthesis (Kirby, 1994). Growth is from intercalary meristems, and internode length increases with successive internodes. The sequence of internode elongation is directly related to leaf emergence, whose rate is determined by thermal time (Kirby *et al.*, 1994). The interval between the extension of successive internodes is one phyllochron (the number of day degrees for a leaf to fully emerge) (Kirby, 1988). Elongation of each internode begins when extension of the previous internode is approximately half-complete (Kirby *et al.*, 1994) and lasts for about 1.5 phyllochrons (Kirby, 1988).

2.2.1.1 Stem diameter and wall width

Crook *et al.* (1994) showed that as the stem developed it became wider and more hollow, with the stem diameter of the basal internodes reaching a maximum value about one month before ear emergence, after which it decreased very slightly before remaining constant until harvest.

Enhanced stem extension is often associated with reduced stem diameter, wall width and stem dry weight per unit length. This has been indicated by Percival (1921), by shading experiments on oats (Mulder, 1954; Holmes *et al.*, 1960) and in the review of lodging in cereals by Pinthus (1973). This suggests that there may be an inverse relationship between longitudinal and transverse growth. Work by Sachs and Kofranek (1963) showed that when the stem growth of *Chrysanthemum morfolium* was promoted with gibberellic acid the stem diameter was reduced. Further

investigation revealed that this was due to fewer and smaller cells across the pith, cortical and vascular tissues. It may also be inferred from this work that the stem wall width will be reduced and that a reduction in the transverse size of the vascular bundles may also result in a reduction of the failure yield stress of the stem. Hence, it appears that stem diameter and wall width (and possibly failure yield stress) are inversely related to the magnitude of stem extension rate. Therefore, an investigation of stem extension rate may elucidate the mechanism by which these plant characters are controlled.

It has frequently been observed that greater stem extension takes place in cereal crops with large canopies derived from either a high nitrogen supply or high seed rate (Mulder, 1954; Holmes *et al.*, 1960; Carles *et al.*, 1960). It is most likely that this response is the plants strategy for shade avoidance (Smith, 1982). It has been demonstrated that this response is triggered by changes in light quality in the form of the ratio of red (R) to far-red (FR) radiation (R/FR) (Morgan and Smith, 1976; Holmes and Smith, 1977c; Smith, 1982). As sunlight is filtered through a canopy there is a parallel reduction in both the flux of photosynthetically active radiation (PAR) and the R/FR ratio (Holmes and Smith, 1977a, b). Plants of shade avoiding species, of which wheat is one, undergo a large increase in stem extension in response to R/FR ratios which have been artificially depressed to represent the qualities of shade light (Morgan and Smith, 1976).

Light quality in terms of R/FR is influenced most by canopy size (Holmes and Smith, 1977b). Measurements of R/FR in different sized wheat canopies have shown that R/FR at ground level is greatly reduced by larger canopies. An increase in the Leaf Area Index (LAI) from 1 to 4 reduced R/FR from 1 to 0.2. In addition there was a linear relationship between logarithm R/FR and LAI in wheat (Holmes and Smith, 1977b). Holmes and Smith (1977b) also found that the spectral energy distribution beneath a canopy was influenced by solar elevation, sky condition, plant age and chlorophyll content.

Solar elevation only affects R/FR on clear days, such that R/FR is decreased as solar elevation decreases (sun becomes closer to the horizon). This means R/FR varies with latitude, time of year and the time of day. Time of day has the largest effect on solar radiation and R/FR, with R/FR values of 0.6 at dawn and dusk compared with 1.2 at solar noon (Holmes and Smith, 1977a). To quantify the effect of time of year on solar elevation and R/FR, the solar elevation at solar noon has been calculated for the extreme dates when stem extension might begin. Angles of solar elevation of 30° and 51° were calculated for 1st March and 1st May respectively (List, 1951). These values would result in R/FR values of about 0.34 and 0.41, using information about the effect of solar elevation on the R/FR ratio at the bottom of a wheat canopy, on a clear day (Holmes and Smith, 1977b). Variation with solar latitude is much smaller e.g. it varies by only 5° at solar noon between the latitudes of 50° and 55° (List, 1951). R/FR values beneath a wheat canopy were increased slightly by overcast skies. They also increased slightly when the crop started to senesce in June, in association with decreasing chlorophyll content (Holmes and Smith, 1977b).

The effect of canopy size on R/FR will depend on its site of reception. Casal and Smith (1988) and Child and Smith (1987) using *Sinapis alba* L. (White mustard), suggest that the receptor of R/FR is both the extending internode and the basal pair of leaves. Work by Lecharny (1979) on the fourth internode of *Chenopodium polyspermum* showed the site of reception to be the internode itself together with the pairs of leaves just above and below this internode. It therefore seems likely that the site of reception is situated within, or close to the extending internode. A rapid promotion of growth has been demonstrated in *Sinapis alba* L. when the internode itself receives low R/FR. The period of stimulus can be as short as one minute, with the growth rate returning to normal approximately 16 minutes after the stimulus has ended (Child and Smith, 1987). A long term promotion of growth is triggered in the most basal internode of *Sinapis alba* L. which can last 24 hours, if the first pair of leaves receive a low R/FR for four hours or more (Casal and Smith, 1988).

So far a relationship in which R/FR decreases as green area index (GAI) increases has been described, and it has been stated that depressed R/FR results in greater stem extension rate. To understand the relationship between R/FR and stem extension rate more fully it is necessary to introduce the mechanism by which the plant detects changing levels of R/FR. Perception of R/FR light quality is by phytochrome (P) (Smith, 1982). With Pr and Pfr absorbing maximally near the red and far-red wavebands respectively, it is clear that phytochrome will be able to perceive some of the R/FR changes in the environment. The relationship between Pfr/Ptotal and R/FR has been shown to approximate a rectangular hyperbole (Smith and Holmes, 1977c), to which a theoretical equation has been fitted (Hayward, 1984).

The logarithmic stem extension rate is linearly related to the phytochrome photo-equilibrium for a number of arable weeds (Morgan and Smith, 1979). The response of stem extension rate to changes in the ratio of Pfr/Ptotal varies among the shade avoiding plant types chosen. *Senecio vulgaris* has a slope for the relationship between logarithmic stem extension rate and Pfr/Ptotal of -0.21, whilst *Sinapis alba* has a slope of -0.13. The rate of stem extension found in the arable weeds studied by (Morgan and Smith, 1979) varied from 0.58 to 0.75 millimetres per degree day (mm $^{\circ}Cd^{-1}$). These compare with extension rates of the lower internodes in wheat of 0.71 to 1.01 mm $^{\circ}Cd^{-1}$ (Kirby, 1988). A base temperature of 0°C was used.

To gain an accurate prediction of stem extension rate from canopy size in wheat, the relationship between Pfr/Ptotal and stem extension rate must be quantified. However, a study of the literature has not found such a relationship, for wheat or any other monocotyledonous plant. This could be due to the difficulty of measuring true stem extension rate in monocotyledonous plants in which the extending shoot apex is hidden within the leaf-sheath until ear emergence. A linear relationship between Pfr/Ptotal and the rate of leaf-sheath extension (rate of height increase, measured to the top ligule) has been found in the grass species *Sporobolus indicus* by Casal *et al.*, (1987). This is good evidence that the extension rate of the leaf-sheath in monocotyledonous plants is linearly related to Pfr/Ptotal. However, this does not

explain the relationship between the extension rate of the true stem and Pfr/Ptotal. Casal (1993) has shown that the extension rate of the first (most basal) internode in wheat is very sensitive to changes in R/FR. By reducing the ratio of R/FR during the photoperiod (midday R/FR values were reduced from 1.0 to 0.6) the extension rate of the first internode was doubled and the extension rate of the second internode was increased by 20%, with subsequent internodes not significantly affected. It must be noted that the R/FR values described here are those above the crop and not at the base of the canopy where the extending internodes perceive changes in R/FR ratios. Nevertheless it is good evidence that the extension rate of wheat internodes is increased by low R/FR values, which in turn are caused by large canopy sizes.

2.2.1.2 Failure yield stress

At the stage when an internode has completed its extension, the stem is mechanically weak and there follows a stage during which the synthesis of structural material occurs (Austin and Edrich, 1975). Crook *et al.* (1994) showed that as the stem developed the thickness of the lignified material increased until ear emergence. This trend was strongly correlated with increasing Young's modulus of elasticity and bending strength. During grain filling the decrease in dry weight of stem sections can be up to 50 % (Kuhbauch and Thorne, 1989), of which 90-100 % of this loss is accounted for by the relocation of water soluble carbohydrates (Austin *et al.*, 1977). The mass of non-soluble compounds (mainly lignin, cellulose and hemicellulose) has been reported to remain nearly constant in a review of carbohydrate storage by Schnyder, (1993). This suggests that very few structural compounds are relocated to the growing ear and that stem failure yield stress will not decrease during the grain filling stage. This is supported by Crook *et al.* (1994) who found Young's modulus and overall stem bending strength to increase until ear emergence, then remain constant during the grain filling period, before declining one or two weeks before harvest.

2.2.2 Varietal and agronomic influences

Significant varietal differences exist for stem bending strength (a similar measure to stem failure moment except the stem has not been taken to failure) (Crook *et al.*, 1994). Genotype strongly influenced stem diameter (Pinthus, 1973; Crook and Ennos, 1995) and stem wall width (Pinthus, 1973). However, a comparison of the lodging resistant variety Riband and the lodging susceptible variety Norman found no statistically significant difference in stem diameter (Travis *et al.*, 1995), although no mention was made as to whether these two varieties are susceptible to stem or root lodging by Travis *et al.* (1995). Easson *et al.* (1993) found crops with high seed rates and high nitrogen applications had basal internodes of small stem diameter and wall thickness. Plant growth regulators increased stem diameter (Crook and Ennos, 1995), however other evidence for this is inconsistent (Green, 1986; Humphries, 1968b).

Studies of failure yield stress have not been found. However, one of its components; Young's modulus of elasticity was significantly higher in a lodging resistant wheat variety than a lodging susceptible wheat variety (Crook and Ennos, 1995). This character was also increased by the application of plant growth regulators (Crook and Ennos, 1995). Few statistically significant differences have been found between the cellulose, hemicellulose and lignin concentrations of cell walls belonging to lodging resistant compared with lodging susceptible wheat varieties, high compared with low nitrogen treatments, and plant growth regulator treatments compared with nil control treatments (Knapp *et al.*, 1987). It was suggested that the arrangement and interaction of the structural carbohydrates and lignin in the stem cell walls may be more important in lodging resistance than the concentrations of these components. Another study has suggested that high levels of soil nitrogen may reduce the thickness of sclerenchyma cell walls and the lignin content of the basal stem (Mulder, 1954), which may reduce failure yield stress.

2.3 AERIAL COMPONENT OF THE MODEL (SINGLE SHOOT)

The lodging risk model calculates the moment which a shoot imposes on its base from height at centre of gravity and the natural frequency of the main stem. Height at centre of gravity is measured as the distance from the stem base to the point of balance on the main shoot, detached of its roots. This plant character consists of a number of components, including the stem height, leaf and stem fresh weight, ear fresh weight and ear length. Natural frequency is the frequency of oscillation of free vibrations of the main stem in response to a deflection caused by a wind gust. Natural frequency acts as the basic controlling parameter of the model for aerial force and draws together a number of plant characters, including the height at centre of gravity, ear weight, stem stiffness and root ball resistance (Baker, 1995).

The height at centre of gravity will be considered first because understanding its growth and development builds on the previous section. The growth and development together with the influence of environment and husbandry on its component parts will then be discussed. Natural frequency will be dealt with subsequently as it is a composite character which is strongly influenced by the height at centre of gravity.

2.3.1 **Growth and development**

2.3.1.1 Height at centre of gravity

Height at centre of gravity increases until harvest due to increasing plant height and ear weight and decreasing stem weight per unit length (Crook *et al.*, 1994). A plant of height 800 mm had a height at centre of gravity of about 400 mm at ear emergence, which increased to about 500 mm at harvest (Crook *et al.*, 1994. The growth and development of the whole stem, stem and leaf weight, ear weight and length will now be considered. The growth of the lower stem has been discussed in section 2.2.1.

Stem height

Stem extension begins between the stages of double ridges and terminal spikelet (Kirby, 1994) and ends soon after anthesis (Kirby *et al.*, 1994). The duration of stem

development is therefore similar to the duration of floral development, which depends on the plants vernalisation requirements, photoperiodism sensitivity and earliness *per se* genes (Worland, 1996). Stem height can be expected to be a function of internode number and internode length. A close relationship between internode number and stem height exists (Kirby *et al.*, 1985a; Stapper and Fischer, 1990; Worland, 1996). Also a highly significant correlation exists between the total leaf number on the main stem and the number of extended internodes, such that a greater number of extended internodes are associated with a greater final leaf number (Kirby *et al.*, 1985b). The length of individual internodes depends on the duration and rate of their extension. The effect of light quality on the extension rate of the basal three internodes has already been covered in section 2.2.1.1, and the same rules might be expected to apply to the remaining distal internodes. An internode extends for approximately 1.5 phyllochrons (Kirby, 1994). Successive internodes grow at approximately one phyllochron intervals with the rate of extension increasing from about 1 mm $^{\circ}Cd^{-1}$ for internode six to about 2 mm $^{\circ}Cd^{-1}$ for internode nine (peduncle) (Kirby, 1988). The final leaf number, extended internode number and thermal duration of internode extension (phyllochron), are affected by sowing date and variety (Kirby, 1994; Kirby *et al.*, 1985b), and are discussed in section 2.3.1.1.

Stem and leaf fresh weight

Stem and leaf fresh weight combined decreased from ten grammes at ear emergence, to six grammes just prior to harvest, to three grammes at harvest (Crook *et al.*, 1994). A similar pattern of development was found for stem fresh weight alone by Easson *et al.* (1993). Few studies have been made of stem and leaf fresh weight, therefore information about stem dry weight has been included as a substitute to give a more complete picture of the growth and development. However, it is acknowledged that caution must be used when applying the following dry weight information to that of stem fresh weight, as these two characters are not directly related at all stages of plant development.

The dry weight of extended internodes increased until two or three weeks after anthesis, mainly due to the accumulation of water soluble carbohydrates (Kuhbauch and Thorne, 1989). During grain filling the stem sections can then lose up to 50 % of their dry weight (Kuhbauch and Thorne, 1989), which probably accounts for most of the fresh weight loss observed by Crook *et al.* (1994). Bush and Evans (1988) found that stem dry weight per unit length could vary four fold in extreme conditions of temperature and radiation; 13 °C and 25.2 MJ m^{-2} day^{-1} compared with 22 °C and 7.9 MJ m^{-2} day^{-1}. These conditions are more extreme than those found in the natural environment. Under natural conditions Bush and Evans (1988) reported the stem dry weight per unit length in wheat to vary between 0.7 to 1.3 mg mm^{-1} over the whole stem. Large variation has also been observed for the stem dry weight of barley by White (1995). Different growing conditions caused the stem dry weight of the bottom two internodes to vary between 0.2 to 0.8 mg mm^{-1}.

Ear fresh weight and length

Ear fresh weight is dependent on the number of grains per ear, individual grain fresh weight and chaff fresh weight. Ear weight and length vary in direct proportion to ear grain number (Friend, 1965a).

In winter wheat a period of vernalisation is required to stimulate the switch from vegetative to reproductive development. The first visual sign of ear development is indicated by the start of spikelet differentiation. The number of spikelets to develop per ear is the product of the rate and duration of spikelet initiation. The number of spikelets initiated varies little over a wide range of conditions, with differences in grain number per ear mainly due to differences in floret formation and survival (Stern and Kirby, 1979; Darwinkel, 1978).

Up to ten florets can be accommodated in each spikelet, although only two or three usually survive. Floret death has been observed between the flag leaf fully expanded and ear peep stages (Siddique *et al.*, 1989), or between the start of ear emergence and anthesis (Kirby, 1988). The length of both of these periods was between 90 and 100

°Cd (0°C base temperature). The survival of florets is believed to depend on the supply of assimilates during this floret death period (Kirby, 1988). Fischer (1985) has shown the 30 day period before 50 per cent anthesis to be critical in determining the number of florets per ear surviving to form grains. Reduced radiation (through shading) and increased temperatures over this period both reduced grain number per ear (Fischer, 1985). It is likely that radiation influenced grain number principally through crop growth rate during the floret death period, with temperature affecting the duration of this period.

This growth phase coincides with the period of stem extension with which the florets compete for assimilates. Consequently a reduction in stem growth due to the Rht_2 dwarfing gene caused an increase in ear growth rate, giving more grains per ear (Brooking and Kirby, 1981). Of the florets which survive most undergo successful pollination to form grains (Sylvester-Bradley and Scott, 1990), unless extremely low or high temperatures are experienced. After anthesis there is a two or three week period of cell division in which the potential size of the grain is set. This initial phase of grain growth is largely by water uptake after which the grains accumulate dry matter until about six weeks after anthesis.

Whether or not the grain realises its potential for grain filling depends on the balance between the "sink" (capacity of the grains in an ear to store assimilate) and the "source" (mainly from current photosynthesis of the ear and culm leaves, but also from stem reserves). If the "source" is not adequate to satisfy the "sink" the grain will not be filled and will appear shrivelled. Consequently, high irradiance levels during this post anthesis period increase grain weight, but the overall effect on yield is less than that found by changing grain number by altering pre anthesis irradiance levels (Evans, 1977). Measurements of ear fresh weight taken on two winter wheat varieties by Crook *et al.* (1994) showed it to increase from about 2 g per ear at ear emergence to about 4 g per ear two weeks before harvest, after which it decreased to about 2.5 g as the ear dried. Easson *et al.* (1993) found greater ear fresh weights which increased from 4.5 g to 7 g before decreasing to 5.5 g just prior to harvest.

2.3.1.2 Natural frequency

To date the only experimental work in which the natural frequency of wheat has been measured is by Griffin (1998). Natural frequency decreased from ear emergence until grain filling, then increased as the grain ripened. Natural frequency was also reduced by weak soil and wet foliage, although the results were inconsistent. Baker (1995) shows that height at centre of gravity is the most important component of natural frequency and the two are expected to be negatively related. As regards the other components of natural frequency, greater values of stem stiffness and root ball resistance are expected to increase natural frequency, and heavy ears are expected to decrease natural frequency.

2.3.2 **Varietal and agronomic influences**

2.3.2.1 Height at centre of gravity

Crook and Ennos (1994; 1995) showed height at centre of gravity to be influenced by variety, increased by high rates of nitrogen and decreased by plant growth regulators. The influence of husbandry factors on the components of height at centre of gravity are now considered.

Stem height

Height differences of up to 15 cm exist between modern recommended wheat varieties (Fenwick, R. 1995, personal communication). It has been suggested by Austin and Jones (1975) that most of the height variation of different varieties is due to variation in internode length rather than internode number. Evidence to support this has been found by Kirby (1994), who demonstrated that varieties differed in the duration over which each internode extended.

Late sown crops are usually shorter than early sown crops (Kirby *et al.*, 1985b; Fielder, 1988; Stapper and Fischer, 1990). This height decrease is often associated with a reduced number of extended internodes (Kirby *et al.*, 1985b; Stapper and Fischer, 1990). Stapper and Fischer (1990) showed that 71% of height variation

found in wheat plants of different sowing dates could be accounted for by the number of extended internodes. Wheat sown on 3 September and 3 December resulted in plant heights of 94 cm and 66 cm, with 6.2 and 4.8 extended internode numbers respectively (Kirby *et al.*, 1985b).

It has already been stated that stem extension usually begins between the stages of double ridges and terminal spikelet. Kirby (1994) has shown that for later sown crops these stages of floral development occur with progressively fewer leaves still to emerge on the main stem. This results in the extension of fewer internodes for late sown crops, and partially accounts for the height differences described. Kirby *et al.* (1985b) and Stapper and Fischer (1990) have also shown that early sown crops begin stem extension close to the double ridges stage of development, whereas late sown crops begin stem extension closer to the later stage of floral development, terminal spikelet. This will add to the effect which sowing date has on the number of leaves to emerge at the start of stem extension, and will result in even fewer internodes extending for later sown crops.

It is apparent that the number of extended internodes can be estimated from the number of leaves still to emerge at the start of stem extension. Good relationships have been observed for the final number of leaves with the number of leaves emerged at double ridges and at terminal spikelet (Kirby, 1994). These two relationships appear to hold over a wide range of environments and varieties (Kirby, 1994). If final leaf number could be predicted, these equations could be used at double ridges or terminal spikelet to estimate the number of leaves (extended internodes) still to emerge (develop). A method of estimating the final number of leaves on the main shoot has been developed by Kirby (1994). This is based on a function of the thermal time from sowing to full vernalisation and the photoperiod at full vernalisation, together with a number of constants which are dependent on variety. Thus, it might be possible to estimate extended internode number at the beginning of stem extension.

To a lesser extent the effect of delayed sowing on reducing plant height is due to decreased internode length, which was found to decrease in proportion with internode number (Stapper and Fischer, 1990). This could be due to the effect of sowing date on the length of phyllochron, which dictates the duration of internode extension. Delaying sowing date from September to February decreased the phyllochron by about 70% (Kirby *et al.*, 1985b). Assuming internode extension rates are not affected by sowing date this would reduce internode length. Kirby (1994) has developed a model to predict rate of leaf emergence (phyllochron) which demonstrates that the rate of change of day length at plant emergence best accounts for the effect of sowing date on phyllochron. In addition, it was shown that variety influences phyllochron without interacting significantly with the sowing date effect. Thus, there is strong evidence for variety and sowing date to affect plant height through internode number and through individual internode length.

High seed rates and high nitrogen applications both increase plant height (Easson *et al.*, 1993; Crook and Ennos, 1995). In addition nitrogen applied early, during the tillering stage, resulted in greater plant heights compared with applications during stem extension (Dobben, 1966). These factors might increase crop height by stimulating the plant's shade avoidance response (2.2.1) which would result in longer basal internodes.

Plant growth regulators can be applied between early stem extension (GS 30) and the late booting stage (GS 45), and can cause height reductions of up to 12 % (Crook and Ennos, 1995). PGRs have three modes of activity; anti-gibberellin activity which shortens lower internodes, production of ethylene compounds which inhibit cell elongation, and amino-acid inhibition which limit the production of new cells (Hay and Walker, 1989). PGRs reduce stem extension most effectively when applied during good growing conditions, consequently products designed to be applied during late stem extension, such as ethylene compounds often produce the greatest height reductions (Crook and Ennos, 1995).

Stem and leaf fresh weight

Crook and Ennos, (1994; 1995) found no differences between the stem fresh weights of six wheat varieties. However, White (1995) found stem dry weight per unit length to be significantly greater in lodging resistant barley varieties compared with lodging susceptible varieties. Increasing the seed rate from 50 to 400 seeds m^{-2} decreased the stem fresh and dry weights from 18 g to 13 g, and 3.8 g to 2.8 g respectively (Easson *et al.*, 1993). Increasing nitrogen applications above 160 kg ha^{-1} reduced both stem weight per unit length (Mulder, 1954) and overall stem dry weight (Crook and Ennos, 1995). The mechanism (2.2.1) by which high seed rates and nitrogen applications might reduce stem dry weight per unit length of the basal internodes may account for these weight differences.

Ear length and fresh weight

Varietal differences have been found for ear fresh weight at the stage of grain filling, ranging from 5.1 g per ear to 6.1 g per ear (Crook and Ennos, 1994; 1995). Stern and Kirby (1979) showed that for a range of sowing dates, there was an inverse relationship between the rate and duration of spikelet initiation. This may account for the insignificant effect of sowing date on grain number per ear found by Kirby (1969). Contrary to this evidence, Jessop and Ivins (1970) found increased grain numbers per ear for later sown crops. In this case the late sown crops had fewer ears per metre squared, which may account for the increased grain number per ear. Grain weight was often unaffected by sowing date (Green *et al.*, 1985), or reduced by later sowing dates by about ten percent (Angus and Sage, 1980). These small effects may be accounted for by variation in developmental rates, which allow crops sown at a typical range of sowing dates to start grain filling at a similar time. However, due to variation in developmental rate other aspects of the crop are often changed e.g. late sown crops often have a smaller biomass and green area, which can reduce the assimilate source, and this may account for the observations of Angus and Sage (1980).

regulators, but sowing date, seed rate and nitrogen application rate had negligible effects.

2.4 AERIAL COMPONENT OF THE MODEL (WHOLE PLANT)

The moment imposed by one shoot and the final shoot number per plant are required to calculate the moment which all the shoots of one plant impose on the plant's anchorage system. The moment imposed by one shoot has been reviewed in section 2.3. Final shoot number per plant can be calculated by dividing the number of ears per metre squared at crop maturity by the plant population per metre squared. The plant population can be measured directly early in the season. Final shoot number per metre squared is determined by the proportion of the maximum shoot number which survive and is therefore influenced by two processes, shoot production and shoot survival. It should be mentioned that the term "shoot" refers to all shoots present in a crop, whilst "tiller" refers to all shoots except main shoots.

2.4.1 Growth and development

Tiller production begins when the third leaf is emerging, which is about 200 $^{\circ}Cd^{-1}$ after seedling emergence (Klepper *et al.*, 1984). It has often been observed to finish when floral initiation begins, between double ridges and terminal spikelet (Thorne and Wood, 1987). The length of this period is influenced by temperature, day length and the date when vernalisation is complete.

Tiller buds are initiated shortly after sowing until the end of leaf primordium initiation, which was mid March for a crop sown on 31 October (Baker and Gallagher, 1983). They are initiated regardless of light intensity and temperature (Friend, 1965b) in the first six leaf axils of the main stem (non-extended nodes). Tiller emergence is in response to thermal time, with the first five tillers emerging at well defined times between 200 and 520 $^{\circ}Cd^{-1}$, assuming unstressed conditions (Klepper *et al.*, 1984). In stressed conditions some tillers may not be produced e.g. the non emergence of the coleoptile tiller is often an indication of poor seed bed quality (Peterson *et al.*, 1982).

Light levels have a strong influence on tiller emergence, with low levels of photosynthetic photon flux density preventing the emergence of some tillers, particularly the coleoptile tiller, and sub tillers which develop from the main tillers (Rickman *et al.*, 1985). As a result a strong relationship exists between maximum shoot number, and the total solar radiation between seedling emergence and double ridges (Evans *et al.*, 1975). Light quality in terms of the R/FR ratio also influences tillering, with low R/FR ratios given at the end of the day causing tillers to be produced more slowly and sometimes for tiller production to stop earlier (Casal, 1988). More specifically low R/FR ratios were found to reduce the number of secondary tillers developing resulting in a higher ratio of primary tillers to secondary tillers. However, final ear number was not affected by R/FR which suggests that light quality affects tiller production but not tiller death. Temperature is another factor which influences whether the emergence of tillers is missed. Higher temperatures restrict the supply of assimilates to tiller buds by increasing the demand for assimilates by the main axis, because of the stimulation of cell division and the increase in rate of leaf primordium formation (Friend, 1962). Water stress during this phase is rare, but reduces the production of tillers when it does occur (Black, 1970).

Little information exists as to what influences the point at which maximum shoot numbers are reached. The end of tiller production and consequent beginning of shoot death has often been found to take place at the start of stem extension, with factors which lead to early ear initiation also leading to an early cessation of tiller production (Fraser and Dougherty, 1977). However, this is an over-simplification. Darwinkel (1978) found maximum shoot number to be reached earlier in high plant density crops than in low plant density crops. This would suggest that maximum shoot number depends upon the balance of supply and demand of assimilates. Factors which affect the supply of assimilates include radiation levels, nitrogen and water supply. The main factors to affect the demand of assimilates include temperature (Friend, 1962) and shoot number per metre squared. From this, a low density plant population would be expected to require a longer period of tillering to reach the maximum shoot

number per metre square which the balance of supply and demand of assimilates can support.

Shoots die between double ridges/terminal spikelet and anthesis (Baker and Gallagher, 1983; Thorne and Wood, 1987). The length of this period is influenced by the plant's vernalisation requirement, temperature and day length. The proportion of shoots surviving is determined by the supply and demand of assimilate over this period (Porter *et al.*, 1984). The supply of assimilate over this period is usually increased by greater radiation, nitrogen and water supplies. Increasing the duration (in days) of the shoot death period through decreased temperature or shorter day length will usually increase the assimilate supply per unit of development. Final shoot numbers are increased when temperature is decreased and radiation increased over the whole growing season (Friend, 1965b). Experiments by Thorne and Wood (1987) have shown that increasing the radiation by 60-100% for 15-20 days before the end of tillering significantly increased the final shoot number. In addition, Evans (1978) showed that increasing radiation during the period 15 to 35 days before anthesis increased final shoot number. However, increasing radiation for 15 to 20 day periods at the beginning and in the middle of the shoot death phases had no effect or only slightly increased final shoot number. Fischer (1985) demonstrated that the proportion of shoots surviving was closely related to the ratio of mean daily incident radiation to mean temperature above 4.5 °C , termed the photo thermal quotient (PTQ), in the 30 days preceding anthesis. Shoot survival is also improved by a plentiful supply of water during stem elongation (Scott *et al.*, 1973).

2.4.2 Varietal and agronomic influences

Varietal differences in maximum shoot number and ear number per metre square have been observed in a review of tillering by Simons (1982). A trend has also been noted for a higher percentage of shoots surviving and greater ear number associated with newer varieties (Austin and Jones, 1975; Simons, 1982).

Deep sowing produces fewer tillers and ears, possibly as a result of reduced coleoptile tillering (Percival, 1921). Later sowing dates have often been associated with fewer ears per metre square, especially for low seed rates (Darwinkel *et al.*, 1977). This observation may be a result of a shorter tillering period resulting in a low maximum shoot number. Alternatively, it may be due poorer plant establishment associated with later sown crops, since low seed rates usually result in smaller shoot numbers per unit area (Darwinkel, 1978). As the plant grows, competition for light and nutrients restrict tiller production leading to shoot death, which is usually much greater for high seed rates (Willey and Holliday, 1971; Darwinkel, 1978). However, these differences in the rate of shoot death are usually insufficient to counteract the effect of plant density, and as a consequence high seed rates usually have greater ear numbers at harvest (Willey and Holliday, 1971; Darwinkel, 1978). Nevertheless the ability of low density plant populations to increase ear numbers through extra tillering is considerable, e.g. a decline in plant density from 400 plants m^{-2} to 100 plants m^{-2} resulted in a relatively small decrease in ear number per metre square from 582 to 430 (Darwinkel, 1978).

The supply of nitrogen can influence final shoot number (Biscoe and Willington, 1984), but its effect also depends on the timing of application (Bremner, 1969). Nitrogen applications of 90 kg ha^{-1} N and 330 kg ha^{-1} N resulted in a final shoot number m^{-2} of 389 and 526 respectively (Biscoe and Willington, 1984). Nitrogen applied during tillering will increase the maximum shoot number, but will also increase shoot death rate, as more shoots will be competing for a diminishing nitrogen supply. Nitrogen applied later will not affect the maximum shoot number, but will improve shoot survival (Bremner, 1969).

The effects of the PGR chlormequat on shoot number have been found to be very inconsistent in a review by Green (1986), but in general it is believed that chlormequat increases shoot production and survival. Matthews and Thomson (1982) have suggested that the increased tiller survival in barley may be a result of a reduction in apical dominance of the main stem which allows the production of more even sized

tillers. This might allow later formed tillers of chlormequat treated plants to compete more successfully with the main shoot and early formed tillers than in untreated plants, on which the size difference between early and late formed tillers is greater. This may lead to increased tiller survival through the more efficient use of resources such as nitrogen. Chlormequat has also been found to delay ear emergence, which may increase the duration of vegetative growth and allow the production of more tillers (Green, 1986). However, Koranteng and Matthews (1982) and Bragg *et al.* (1984) found no increase in the duration of tiller production due to chlormequat. This suggests there is an increase in the time between tillering and ear emergence, which would allow a greater chance for assimilation to take place and support tiller survival.

In summary, final shoot number per plant is influenced primarily by its two components plant density and shoot number per unit area. Plant density has a large influence on final shoot number per plant due to the crop's ability to compensate for low plant densities through extra tiller production and maintenance. A number of processes are involved in the determination of final shoot number per unit area which rely considerably on the supply of assimilates to the shoots during the tiller growth and tiller death phases. The amount of radiation intercepted and nitrogen supply are the most important factors controlling the supply of assimilates and genotype will modify the effect of these two factors.

2.5 ROOT ANCHORAGE COMPONENT OF THE MODEL

This component of the model is calculated from the structural rooting depth and the root plate spread. These two parameters develop concurrently and will be considered together. Crook and Ennos (1993) have described how the pattern of crown root development forms a "root cone" (Figure 2.1). The base of this root cone is defined as the point along the crown root at which it ceases to be rigid (stiff) enough to provide anchorage. The structural rooting depth is the depth of soil to which the base of this root cone extends. This parameter is a function of the crown depth, the length of rigid root, and angle of root spread. Root plate spread is the width of the root

cone base. This parameter is a function of the width of the plant base at soil surface, the length of rigid root and the angle of root spread.

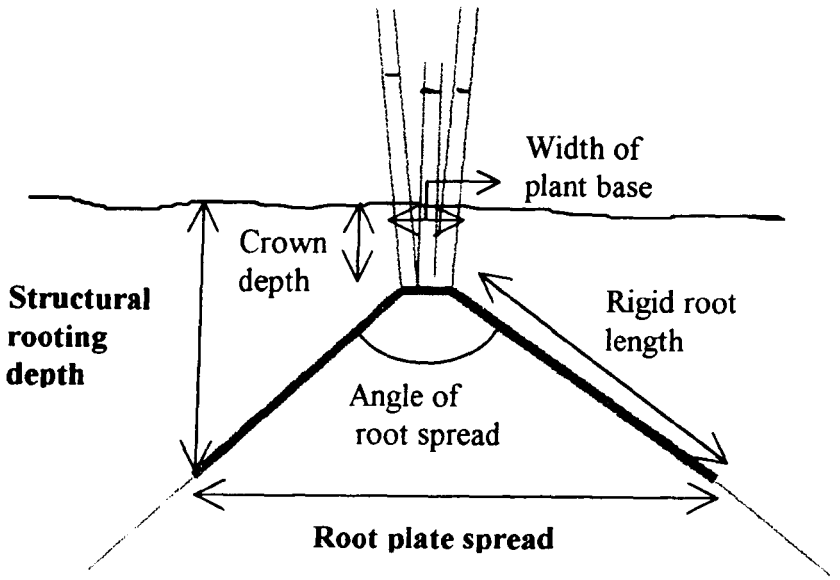

Figure 2.1 Anchorage system of a wheat plant.

2.5.1 Growth and development of the roots and crown

The first visual evidence of germination is the emergence of three to six seminal roots which develop from the radicle of the seed. The appearance of all six has been recorded to take place within six weeks (Gregory, 1978). They are usually devoid of hairs, have very little soil attached and have a diameter of 0.5 to 0.7 mm (Ennos, 1991). It has been suggested that the function of the seminal root system is to supply the seedling with nutrients and is therefore only temporary (Nelson, 1946). However, other studies have shown the seminal root system to persist until harvest (Gregory, 1978). Taking into account their are small number and weak physical properties it seems likely that these roots play a minor role in anchoring the plant.

Ennos (1991) has shown that the anchorage of spring wheat is mainly dependent on the thick basal regions of crown roots. Crown roots develop next from the unextended nodes which remain below ground to form the crown. Generally this

involves the lowest six nodes although this number can vary according to variety, sowing date and weather (Kirby, 1994). Up to four roots can be produced at each crown node, although only two are usually found in practice (Klepper *et al.*, 1984). Crown roots also develop from the 'below ground' nodes of tillers in a similar pattern to that described for the subterranean nodes of the main stem (Klepper *et al.*, 1984). However, it is also important to remember that the death of these tillers will result in the death of their associated crown roots (Gregory, 1978). Crown root development begins at a particular node three phyllochrons after its leaf has emerged. Crown root number per plant increases exponentially with thermal time between emergence and stem elongation (Vincent and Gregory, 1989). This means that for an early sown crop a proportion of the crown roots develop during the autumn. Because of the strong relationship between root development and the production of leaves and tillers, leaf number can be used to predict the potential number of crown roots on any culm (Klepper *et al.*, 1984).

According to Austin and Jones (1975), complex plant responses form part of an integrated control system by which the seedling can alter the length of its sub crown internode to keep a stable crown depth with different drilling depths. Poulos and Allan (1987) observed that for deep sowings the sub crown internode length was positively related with different seed depths, but crown depth remained relatively constant. However, for shallower drillings a sub crown internode did not usually develop and crown depth was positively related to seed depth. More recently Kirby (1993) showed that crown depth increased to 40 mm for sowing depths up to 68 mm, but for seed depths greater than 68 mm crown depth remained reasonably stable at 40 mm. This was similar to the findings of Loeppky *et al.* (1989), who also found a difference in crown depth due to sowing date which was attributed to a difference in response to temperature. Deep sowings which have a sub crown internode cause the seminal roots to be separated from the crown. They can also cause the development of a 'double anchorage' due to the formation of two or three crown roots at the coleoptilar node, next to the seed (Klepper *et al.*, 1983).

Lupton *et al.* (1974) suggested that soil and climatic conditions influence root growth more than the genetic makeup of the plant material. Soil with few pores of a diameter suitable for unimpeded root extension and a high bulk density reduced the extension of the seminal roots leading to a shallower seminal root system (Finney and Knight, 1972). Interestingly, the growth of the crown roots was not affected by greater soil bulk density. However, Ellis and Barnes (1980) showed greater root counts per plant in compacted soil of direct drilled plots than on ploughed plots at early stem elongation; By anthesis these differences had disappeared, because of more rapid growth on the ploughed plots. The initiation of roots can be prevented by unfavourable soil conditions such as drying and crusting of the soil surface (Troughton, 1980). Kmoch *et al.* (1957) found root growth to be more extensive in moist soil, with finer and more branched roots developing under dry conditions.

At the end of a waterlogging period between mid-January to mid-April Cannell *et al.* (1985) showed that root lengths of winter oats were reduced by 77 % but root density in the top ten centimetres was increased, compared with roots grown in freely drained soil. When growing in poorly aerated conditions water logged roots can develop aerenchymatous tissue, which allows sufficient oxygen to be obtained from the aerial parts of the plant for crown roots to grow several centimetres into the waterlogged soil (Cannell *et al.*, 1985). By anthesis root lengths of the waterlogged plants were only ten per cent less than those grown in freely draining conditions.

Total root biomass appears to be reduced by low R/FR ratios (Knauber and Banowetz, 1992). Decreasing R/FR ratios, typical of those found within wheat canopies (1.2 - 0.5), reduced the shoot dry weight per plant through decreased tillering. In addition, decreasing R/FR ratios increased the shoot/root ratio. However, the R/FR ratios which influenced the shoot/root ratios were outside the range normally found within wheat canopies (4 - 1.2) (the effect of typical R/FR ratios were not tested). This indicates that low R/FR, caused by large canopies, could reduce root dry weight proportionally more than it reduces shoot dry weight and therefore may reduce plant anchorage.

It is well documented that total root dry weight continues to increase until anthesis (Gregory, 1978; Welbank *et al.*, 1974). However, this information includes the distal parts of the root system which play no part in anchorage. It has been shown that development of the structural parts of the root system finishes close to the booting stage (Crook *et al.*, 1994). After this root bending strength and anchorage strength remained relatively constant (Crook *et al.*, 1994). From this it may be suggested that the maximum length of rigid root is reached at the booting stage (GS 40).

Analysis of the mature wheat plant root system has shown the basal regions of the roots to have a diameter of 1-3 mm which taper to 0.6 - 0.8 mm about 40 mm from their base (Ennos, 1991). Similarly, Easson *et al.* (1995) found the cross sectional area of the roots to decrease from 1.5 to 0.5 mm^2 between the 0 - 40 mm and 40 - 80 mm sections of the root. The basal region of the root not only has a lignified stele, but also a ring of lignified material around its perimeter which is not present on more distal regions of the crown root (Ennos, 1991). It has been suggested by Ennos that this extra lignification is responsible for the increased stiffness of the basal regions of the crown root which provide anchorage. The basal region of the root is also unbranched and covered in root hairs with a rhizosheath of soil. This can increase the diameter to 5 mm (Ennos, 1991) and makes the stiff region of the root, which provides anchorage, easy to identify.

The width of the plant base is likely to affect the root plate spread by determining the position at which the structural roots initiate. If two plants with the same angle of spread and rigid root length differ in their width of plant base by 20 mm, then the root plate spread will also differ by 20 mm. It is likely that shoot number per plant will be the main factor which influences this parameter, with high shoot numbers per plant associated with wide plant bases. Plant posture could also be important, with a postrate habit causing larger plant base widths than erect habits. Finally, there is no evidence to suggest that angle of root plate spread changes during its development (Pinthus, 1973).

2.5.2 Varietal and agronomic influences

No literature has been found which concerns structural rooting depth directly, however there is information about its components; crown depth, rigid root length and angle of root spread which may be of use. Genotype influences crown depth (Poulos and Allan, 1989) and angle of root spread (Pinthus, 1967; Crook and Ennos, 1994; 1995). However, a thorough investigation of angle of root plate spread by Pinthus (1967) showed it to be unaffected by other factors, including seed depth, plant density and soil type. Crown depth was decreased by shallow drilling depths, but was not affected by deep drilling (Poulos and Allan, 1987). The seed treatment 'Baytan' increased crown depth by retarding growth of the sub crown internode (Montfort *et al.*, 1996). Low seed rate crops produced crown roots with a greater diameter and tensile strength (Easson *et al.*, 1995), which may indicate that low seed rates would also increase rigid root length. High nitrogen applications reduced root bending strength (Crook and Ennos, 1994; 1995), a rooting character similar to root rigidity. This may indicate that high nitrogen supplies could reduce rigid root length. No evidence has been found for plant growth regulators to influence structural rooting depth or its components.

Root plate spread is strongly influenced by genotype (Pinthus, 1967; Crook and Ennos, 1994, 1995). This could be through its influence on the angle of root plate spread (Pinthus, 1967; Crook and Ennos, 1994; 1995) or root bending strength (Crook and Ennos, 1994; 1995). Low seed rates and low nitrogen rates may increase rigid root length, which would result in a greater root plate spread. Large root plate spreads have been tentatively associated with wide plant bases, which result from high shoot numbers per plant. From this it may be inferred that factors which increase shoot number per plant, such as low seed rates, may increase root plate spread. Plant growth regulators have been shown to have no effect on "root cone" or root strength properties (Crook and Ennos, 1995; Easson *et al.*, 1995). This is contrary to claims made by some PGR manufacturers, and it must be noted that not all PGR types have been investigated. There is some doubt as to whether chlormequat increases crown root production, and if so by what mechanism. Humphries (1968a) and Hanus (1970)

demonstrated chlormequat to increase total root length and root dry matter, but made no reference to the anchorage parts of the root system. It has been shown that chlormequat may enhance tiller survival (Koranteng and Matthews, 1982; Kettlewell *et al.*, 1983), which may enlarge root plate spread by increasing the plant base width. However, Bragg (1982) found no effect on shoot or root number after applying chlormequat at GS 23.

2.6 LITERATURE REVIEW SUMMARY

All of the main plant characters associated with lodging (stem base diameter, stem wall width, failure yield stress, height at centre of gravity, natural frequency, shoot number per plant, structural rooting depth and root plate spread) continue to develop after the beginning of stem extension, with final values of natural frequency and height at centre of gravity not realised until after anthesis. It is therefore likely that prediction schemes need to be developed to link early spring crop observations with the summer-time values of all these plant characters. Variety choice and husbandry practice influence all of the plant characters studied. In addition these agronomic decisions generally influenced the plant characters more than environmental factors.

The geometrical components of stem failure moment; stem diameter and wall width have been observed to be inversely related to the size of the wheat canopy during early stem extension. This is probably because the stems extend more quickly (etiolate) in shaded conditions, resulting in narrower stems with thinner stem walls. This may explain why husbandry practices which cause large spring canopies have often been associated with weak stems. Stem failure yield stress continues to develop until ear emergence, which is some time after stem diameter and wall width have reached their final values. Less is known about this plant character but its value may be associated with vascular bundle number, width of the sclerenchyma layer and the proportions of lignin, cellulose and hemicellulose present in the cell wall. Stem failure yield stress may also be related to the rate of stem extension, similar to stem diameter and wall width.

The plant characters used to calculate aerial force of a shoot are natural frequency and height at centre of gravity. Natural frequency has not yet been measured in wheat. It is expected to be influenced by height at centre of gravity, ear weight, stem stiffness and root ball resistance. Height at centre of gravity is determined by stem height, leaf and stem fresh weight, ear fresh weight and ear length, none of which reach their final value before anthesis. Stem height is influenced most by genotype and sowing date, stem and leaf fresh weight appeared to be influenced most by seed rate and nitrogen supply, and ear weight and length are influenced most by seed rate.

The aerial force of the whole plant is calculated from the aerial force of a single shoot and the shoot number per plant. The final number of shoots per plant is not reached until anthesis and depends upon the plant and shoot densities. Plant density is mainly determined by seed rate and can be ascertained early in the season. Shoot density appears to be dependent upon the supply and demand of assimilates during the tiller death phase, of which genotype, nitrogen and radiation supplies are major influencing factors.

Anchorage failure moment is calculated from structural rooting depth and root plate spread, whose development probably finishes at around ear emergence. Soil conditions such as bulk density and moisture content have a large influence on root development. The main agronomic influence on the structural rooting characters is genotype, which affects crown depth, angle of root spread and rigid root length. Shallow drilling depths can reduce crown depth, and it appears likely that low plant densities result in greater rigid root lengths.

2.7 THE EXPERIMENTS

The development of schemes to predict the summer-time values of lodging-associated plant characters from early season plant measurements and field observations is central to achieving the main thesis aim. First, it would be advantageous to

understand how these plant characters develop over the growing season with respect to influencing factors of site, season, variety and husbandry. A study of the literature showed that only a rudimentary knowledge exists for most of the lodging-associated plant characters as to their developmental patterns and response to environmental and agronomic factors. Therefore, experiments were set up to extend the understanding of growth and development of lodging-associated plant characters. The influence of the main factors were investigated except the influence of site, which could not be studied due to limited resources.

2.7.1 The experiments and treatments

An array of treatments that encompass the important elements of crop husbandry were established in the 'main experiment' to produce a wide range of crop structures, which also had different lodging risks. Husbandry treatments deemed to have the largest influence on lodging were investigated. These included early and late sowing dates, high and low seed rates and high and low levels of soil residual nitrogen.

An early sowing date was expected to produce a taller, more forward crop, with a larger canopy, which would provide a higher lodging risk than the later sown crop. A high seed rate was expected to produce a high plant density crop with tall, weak stems and few roots per plant, which should provide a higher lodging risk than the low seed rate crop. The high level of soil residual nitrogen was designed to emulate either high soil residues left from the previous break crop or the practice of applying organic manure/slurries before sowing, both of which are thought to increase lodging risk. It is acknowledged that other husbandry practices such as drilling depth and the seed treatment 'Baytan' influence lodging, but these were valued as less important and therefore not investigated in this experiment.

The most important methods of lodging control were also compared. These included the most widely used types of early and late applied plant growth regulators (PGRs) and a 'Canopy Management' control treatment. A nil lodging control treatment provided a standard against which lodging control methods could be compared.

The early PGR treatment, applied at the beginning of stem extension was expected to reduce lodging risk by inhibiting extension of the lower internodes and so reducing plant height. The common perception of this treatment is that it also reduces stem lodging risk by strengthening the lower internodes. The early PGR followed by the late PGR treatment applied at the 'boots swollen stage' was designed to reduce the moment which the aerial part of the plant imposes on its base even more by inhibiting extension of the upper internodes. The 'Canopy Management' treatment was designed to reduce canopy size and lodging risk by adding optimum amounts of nitrogen only. The theory behind 'Canopy Management' is that medium sized canopies (Sylvester-Bradley *et al.*, 1997) can intercept 95 % to 100 % light (Monsi and Saeki, 1953) and should therefore, achieve near maximum potential yields. The majority of conventionally fertilised crops have the potential to reach a green area index (GAI) greater than five by ear emergence (Sylvester-Bradley *et al.*, 1998a). This means that there is scope for spring nitrogen applications to be used to control potential canopy size, mainly by influencing shoot number. The idea behind this treatment was to produce a crop with a moderate canopy size, whilst incurring little or no yield reduction, which at the same time lessened lodging risk by reducing the moment which the aerial part of the plant imposed on its base. Spring rolling is another recognised method of lodging control. However, this was not investigated due to its infrequent practice in comparison to other lodging control methods.

A 'variety experiment' was set up to test the varietal range of lodging-associated plant characters and to investigate whether the prediction schemes set up for a single variety in the main experiment could be used with other varieties. To do this, varieties with a wide range of physiological traits and perceived lodging risks were studied. This variety experiment was also used to understand why varieties have different lodging risks. Ideally, information about lodging-associated plant characters is required for all varieties, but time limitations prevent this aim from being realised. Therefore, a core subset of varieties with a range of lodging-associated traits and

lodging risks was investigated. In addition to the core subset varieties, measurements were taken on as many other varieties as time allowed.

2.7.2 The measurements

Growth stage dates and measurements for basic growth analysis are required throughout the season to describe the general growth and development of the crops. These included plant population and shoot number per unit area, with dry weight, fresh weight and GAI partitioned for leaf, stem and ear. To understand the growth and development of lodging-associated characters for different husbandry treatments, stem diameter, stem wall width, stem failure yield stress, height at centre of gravity, natural frequency, shoot number per plant, root plate spread and structural rooting depth were measured thoughout the season for all treatments. The literature review has also highlighted a number of additional plant characters which are either components or potential predictors of the main lodging-associated plant characters. Therefore, measurements of crown depth, crown width, plant diameter at soil surface, crown root number, rigid root length, root cone angle, height, plant fresh weight, ear area and ear fresh weight were made throughout the season.

3. MATERIALS AND METHODS

3.1 THE EXPERIMENTS

3.1.1 Experimental site

The experimental work was conducted at ADAS Rosemaund Research Centre, Preston Wynne, Hereford. The main experiments (MT95 and MT96) were carried out over two years; the 1994-95 and 1995-96 seasons. The variety experiment (VT95) was carried out in the 1994-1995 season. For experimental site details see sections 3.1.5 and 3.1.6.

ADAS Rosemaund was chosen as the site at which to conduct the experiment for specific reasons. Firstly, Rosemaund has silty clay loam soils, retentive of nutrients and moisture, which promote high yielding crops with large leaf canopies. Secondly, Rosemaund is situated in the West of the country, which has a higher average rainfall than the East. Both these factors were expected to increase the chances of lodging occurring during the experimental programme.

3.1.2 Experimental design

The main experiment was a split split plot design with time of sowing treatments on main plots, seed rate treatments on sub-plots and residual nitrogen and lodging control treatments on sub-sub-plots. Individual sub-sub-plot sizes were 4m x 18m for MT95, and 4m x 24m for MT96. There were three replications of each treatment combination arranged as three blocks giving 96 plots. VT95 was a randomised block, with four replications and plot sizes of 1.8m x 21.0m. For experimental plans see Appendix 2.

3.1.3 Experimental treatments

3.1.3.1 The main experiment

The variety used in the main experiment was Mercia. Mercia is a non semi-dwarf variety which possesses moderate to poor standing power (National Institute of Agricultural Botany (NIAB) standing power rating = 6; NIAB, 1996). It has a moderate yield and good bread-making quality, and has been fully recommended by the NIAB from 1986 to 1996. Mercia is used as a benchmark variety in other HGCA-funded physiology research projects including the 'Development' and 'Crop intelligence' projects, which have provided a comprehensive description of the growth and development of Mercia in a wide range of sites and seasons (Sylvester-Bradley *et al.*, 1998a).

To provide a wide range of crop structures and crops with a range of lodging risks, different sowing dates, seed rates and nitrogen residues were tested in all combinations. Within each of these treatment combinations were four sub-sub-plots on which were compared treatments expected to control lodging risk. Thus, crops which received an early PGR, early and late PGR and a 'Canopy Management' treatment were compared with a crop which received no lodging control measures.

'Early' and 'late' sown crops were scheduled for late September and mid-late October respectively. Seed was drilled at both 'high' (500 seeds m^{-2}) and 'low' (250 seeds m^{-2}) seed rates. Seed rates were not adjusted for different establishment conditions caused by variable seed bed quality and sowing date. Two levels of nitrogen were applied to the previous crop (spring oilseed rape) before it was harvested. In the MT95 experiment, 330 kg ha^{-1} N and 30 kg ha^{-1} N were applied to create the 'high' and 'low' residual nitrogen levels respectively. In the MT96 experiment, 350 kg ha^{-1} N was applied for the 'high' level and 50 kg ha^{-1} N applied for the 'low' level. The three lodging control treatments included an early PGR treatment, an early PGR followed by a late PGR treatment and a 'Canopy Management' treatment. These

treatments were compared with untreated plots and with each other. The early PGR treatment was an application of new '5C Cycocel' (chlormequat + choline chloride) at the ear at one centimetre stage (GS 31). The early PGR followed by a late PGR treatment was new '5C Cycocel' at GS 31, plus an application of 'Terpal' (2-chloroethylphosponic acid + mepiquat chloride) at the 'boots swollen' stage (GS 45). The 'Canopy Management' treatment was designed to produce a canopy with a green area index of five by the end of May (ear emergence), and then to maintain the canopy for as long as possible through grain filling (Sylvester-Bradley *et al.*, 1997). Canopy size is measured as the Green Area Index (GAI), which is the ratio between the total area of all green tissues, viewed from one side, and the area of ground they occupy. To attain the target canopy size of five, the application of nitrogen at both early and main dressings was tailored according to the spring soil and crop nitrogen contents. The amount of nitrogen applied was calculated by assuming that 30 kg ha^{-1} N was required to build each GAI unit and that the plant could take up nitrogen fertilizer with a 60 % efficiency. In the MT95 experiment this was followed by an additional, late application of 60 kg ha^{-1} N at anthesis to maintain the canopy through grain filling. For experimental site details see section 3.1.5.

3.1.3.2 Variety experiment

VT95 tested 20 varieties which had a wide range of physiological traits including rate of development, height, tillering and lodging risks (Table 3.1). A detailed investigation was carried out on a core subset of varieties, which included a very tall, poor standing variety (Little Joss), a short, moderate standing variety (Beaver), a medium height, moderate standing variety (Mercia, the variety used in the main experiments), and two short, good standing varieties (Riband and Hereward). A less detailed investigation was carried out on 15 other varieties (Table 3.1). See section 3.1.6 for experimental site details.

Table 3.1 A description of varieties used in the VT95 experiment.

Variety	Standing power	Straw shortness	Gibberellic acid reaction	Day-length sensitivity	Tiller production	Tiller survival
Little Joss	POOR	TALL	R	S		
Maris Huntsman	5	3	R	S	M-H	L
Longbow	5	6	R	S	H	M-H
Apollo	6	5	I	S	M-H	H
Beaver	6	8	R	S	H	H
Cadenza	6	4	R	S	H	M-H
Mercia	6	6	R	S	M-H	H
Norman	6	7	I	S		
Rialto	6	6	R	S	H	M
Avalon	7	7	I	S	M-H	L
Brigadier	7	8	I	S	H	H
Hunter	7	7	I	S	H	M-H
Soissons	7	7	I	I	L	H
Spark	7	5	R	S	H	M-H
Hereward	8	8	I	S	H	L
Riband	8	8	I	S	M	M-H
Ami (Non UK)	-	-	I	I	-	-
Avital (Non UK)	-	-	R	I	-	-
Florin (Non UK)	-	-	-	-	-	-
Scipion(Non UK)	-	-	-	-	-	-

Standing power: 5 = poor, 8 = good (NIAB, 1978-1995)

Straw shortness: 3 = tall, 8 = short (NIAB, 1978-1995)

Gibberellic acid reaction: R = responsive, I = insensitive (Worland *et al.* 1994)

Daylength sensitivity: S = sensitive, I = insensitive (Worland *et al.* 1994)

Tiller production: H = high, L = low (J. Foulkes, personal communication)

Tiller survival: H = high, L = low (J. Foulkes, personal communication)

3.1.4 Site management

For each experimental year the whole site was ploughed prior to the first time of sowing. The area for each time of sowing treatment received secondary cultivation just before drilling to produce a fine tilth. The drill was calibrated for high and low seed rates before drilling, with discards drilled at the low seed rate.

A prophylactic programme of disease, weed and pest control was used for all the experiments. Treatments were therefore dependent upon the diseases, weeds and pests encountered locally (HGCA Development contract R & D protocol, 1994). See Table 3.2 and Table 3.7 for site records.

3.1.5 Main experiment field records

Table 3.2 Site records of the MT95 and MT96 experiments

Experiment	MT95	MT96
Field name	Belmont	Jubilee
Field altitude (m)	84	84
Soil texture & series	Bromyard- stoneless silt clay loam Middleton - stoneless silty loam	Bromyard - stoneless silt clay loam
Drainage	Bromyard - well drained Middleton - seasonal waterlogging	Bromyard - well drained
Soil analysis pH	7.4	7.1
P, K, Mg : mg/l (Index)	32 (3), 242 (2), 117 (3)	74 (5), 428 (4), 125 (3)
Organic matter %	2.8	2.9
Previous cropping	1993 Spring Oilseed rape 1992 Spring Barley / Spring Oats 1991 Winter wheat	1994 Winter oilseed rape 1993 Winter wheat/ winter barley 1992 Winter wheat
Cultivations **Early sowing** **Late sowing**	Ploughed 12/9/94 Power harrow x1 23/9/94 SKH crumbler x2, power harrow x1 17/10/94	Ploughed 18/9/95 Power harrow x1 20/9/95 Power harrow x1 01/11/95
Drilling date	Early sowing 23/9/94 Late sowing 17/10/94	Early sowing 20/9/95 Late sowing 01/11/95
Drill type & width	Accord drill, 4 m width	Accord drill, 4 m width
Seed rate	500 seeds m^{-2}=201.1 kg ha^{-1} 250 seeds m^{-2}=100.6 kg ha^{-1}	500 seeds m^{-2} = 233.0 kg ha^{-1} 250 seeds m^{-2} = 116.5 kg ha^{-1}
TGW of seed (g)	39.98	46.60
Row width	12 cm	12 cm
50% Emergence date	Early sowing 3/10/94 Late sowing 3/11/94	Early sowing 01/10/95 Late sowing 22/11/95
Herbicides	Javelin Gold (5.0 l ha^{-1}) 16/11/94	Javelin Gold (2.0 l ha^{-1}) & Isoproturon (1.0 l ha^{-1}) Ally (30 g/ha) 1/5/96 Cheetah (2.5 l ha^{-1}) & Starane (0.5 l ha^{-1}) 9/5/96
Fungicides	Tern (0.75 l ha^{-1}) & Sportak 45 (0.9 l ha^{-1}) 13/4/95 Corbel CL (2.5 l ha^{-1}) 18/5/95 Legend(0.7 l ha^{-1}) & DerosalWDG (0.2kg ha^{-1}) 9/6/95	Tern (0.75 l ha^{-1}) & Sportak 45 (0.9 l ha^{-1}) 1/5/96 Folicur (1.0 l ha^{-1}) 30/5/96 Silvacur (1.0 l ha^{-1}) & Patrol (0.5 l ha^{-1}) 22/6/96
Insecticides	Decis (200ml ha^{-1})16/11/94 Phantom (100g ha^{-1}) 28/6/95	Draza (5.5 kg ha^{-1}) 19/10/95 Metarex (7.7 kg ha^{-1}) 3/11/95 Cypermthrin (0.25 l ha^{-1}) 1/3/96
Harvest date	11/8/95	19/8/96

3.1.5.1 Nitrogen fertiliser applications

Nitrogen was applied as ammonium nitrate ('Nitram', 34.5% nitrogen) and spread on the experiments by hand, if a treatment, or by farm spreader. For the nitrogen applications used to create the residual nitrogen treatments, see section 3.1.3. Nitrogen rates were based on ADAS recommendations for the soil type and nitrogen index (MAFF, 1983). For the different levels of residual nitrogen, 'high' was deemed to be nitrogen index 1 and 'low' was nitrogen index 0. For a late developing crop 10 kg ha^{-1} N less than the above recommendations were applied (Sylvester-Bradley, R., personal communication). The MT95 and MT96 experiments had a small nitrogen dressing in March, followed by the main nitrogen application close to GS 31. These applications were applied to all treatments apart from the 'Canopy Management' treatment. See Table 3.3 and Table 3.4 for nitrogen applications to the 'normal nitrogen' treatments, and Table 3.5 and Table 3.6 for nitrogen applications to the 'Canopy Management' treatment.

Table 3.3 MT95 nitrogen fertiliser applications (kg ha^{-1} N) for all 'normal nitrogen' treatments.

	Early sown high residual N	Early sown low residual N	Late sown high residual N	Late sown low residual N
08/3/95	30	30	30	30
04/4/95	120	170	-	-
13/4/95	-	-	110	160

Table 3.4 MT96 nitrogen fertiliser applications (kg ha^{-1} N) for all 'normal nitrogen' treatments.

	Early sown high residual N	Early sown low residual N	Late sown high residual N	Late sown low residual N
14/3/95	40	40	40	40
04/4/95	110	160	-	-
29/4/95	-	-	100	150

Table 3.5 MT95 nitrogen fertiliser applications (kg ha^{-1} N) for the 'Canopy Management' lodging control treatment.

	Early sown high residual N	Early sown low residual N	Late sown high residual N	Late sown low residual N
04/4/95	-	80	-	-
13/4/95	-	-	30	30
26/4/95	-	-	-	50
05/5/95	50	-	20	-
12/6/95	60	60	60	60

Table 3.6 MT96 nitrogen fertiliser applications (kg ha^{-1} N) for the 'Canopy Management' lodging control treatments.

	Early sown high residual N	Early sown low residual N	Late sown high residual N	Late sown low residual N
11/3/96	-	-	-	30
02/4/96	-	50	-	-
17/4/96	-	-	-	60
08/5/96	-	-	-	40

3.1.5.2 Plant growth regulator applications

The PGRs 5C Cycocel and Terpal were applied to the designated treatments (3.1.3.1) at GS 31 and GS 45 respectively for both MT95 and MT96 experiments. MT95 had 5C Cycocel applied to the early and late sown treatments on 24 March 1995 and 10 April 1995 respectively, at a rate of 2.5 l ha^{-1}. Terpal was applied to both sowing date treatments on 20 May 1995, at a rate of 1.5 l ha^{-1}. MT96 had 5C Cycocel applied to the early and late sown treatments on 3 April 1996 and 25 April 1996, at a rate of 2.5 l ha^{-1}. Terpal was applied to the early and late sown treatments on 2 June and 7 June 1996 respectively, at a rate of 1.5 l ha^{-1}. For the MT95 experiment GS 45 occurred on the same date for both sowing date treatments, but on different dates in MT96. Therefore, Terpal was applied on one date in MT95 and on two dates in MT96.

3.1.6 Variety experiment field records

Table 3.7 Site records of the VT95 experiment

Field name	Drive Meadow	
Field altitude (m)	84	
Soil texture & series	Bromyard - stoneless clay loam silty	
Drainage	Well drained	
Previous cropping	Linseed	1994
	Winter Wheat	1993
	Winter Oilseed Rape	1992
Cultivations	Ploughed	11/10/94
	Power harrow x1	12/10/94
Drilling date		12/10/94
Drill type & width	Accord drill, 2.0 m width	
Seed rate	350 seeds/m2	
Herbicides	Panther (2.0 l ha^{-1})	17/11/94
	Starane 2 (0.75 l ha^{-1})	15/5/95
Fungicides	Sportak 45 (0.9 l ha^{-1})	08/4/95
	Tern 750 EC (0.75 l ha^{-1})	08/4/95
	Folicur (1.0 l ha^{-1})	18/5/95
	Silvacur (1.0 l ha^{-1})	16/6/95
Insecticides	Cyperkill (0.2 l ha^{-1})	17/10/94
	Phantom (100 g ha^{-1})	26/6/95
Molluscicides	Draza (5.5 kg ha^{-1})	28/10/94
Harvest date		08/8/95

VT95 had 63 kg ha^{-1} N applied on 22 March 1995. This was followed by 147 kg ha^{-1} N on 28 April 1995 and 40 kg ha^{-1} N applied as foliar urea on 6 July 1995. 5C Cycocel was applied on 8 April 1995 at 2.5 l ha^{-1}.

3.2 PLANT MEASUREMENTS

3.2.1 Plant sampling

Plant population counts were carried out soon after full emergence. Plants were counted in the row either side of a 0.5 m bar placed between the rows. Three such counts were made in each plot. Final plant populations were determined at GS 30 by excavating and counting all plants contained within a 0.72 m^2 quadrat.

Two methods of plant sampling were used; 0.72 m^2 (1.2 m x 0.6 m) quadrat samples for growth analysis and a sample of ten plants (including structural roots), for detailed lodging specific measurements. Plant growth stages were defined using the method of Tottman and Broad (1987). All the treatments of the main experiments were sampled at growth stage (GS) 30, GS 31, GS 33, GS 39 and GS 69-73. Subsets of the treatments were sampled at extra growth stages (see Appendix 3). The variety experiment was sampled at GS 31, GS 39 and GS 61 + 75 $°Cd^{-1}$ (base temperature of 0°C). Details of sampling dates, treatments sampled and the measurements taken in the main and variety experiments are given in Appendix 3.

The protocol for determining sample areas is given in Sylvester-Bradley *et al.* (1998b). To avoid local bias in selection of samples, sampling was carried out from pre-determined areas by placing quadrats in the field prior to sampling. Quadrats were positioned at least 0.5 m apart and at least three rows from the edge of the plot or tramlines to avoid sampling plants influenced by the 'edge effect' (Watson and French, 1971). To avoid systematic bias, each plot was sampled at a different point along its length. Each quadrat was oriented so that one row of plants passed through diagonal corners of the quadrat. At early growth stages (up to and including GS 31) the plants were dug up with their roots, which were later cut off and discarded in the laboratory. At later growth stages the above ground material was cut off at ground level in the field. The objective was to recover all above ground plant material. Once sampled, the plant material was placed in labelled plastic bags which were sealed to prevent drying, and the samples were stored at 4°C until analysis.

Ten plants were selected randomly from around the edge of the quadrat area. Two plants were dug from each of the two short quadrat sides and three plants dug from each of the two long quadrat sides, to give a total of ten plants. Care was taken during plant extraction to ensure that the structural crown roots were completely recovered. The plants were then placed in plastic bags and stored at 4°C, until analysis.

3.2.2 Growth analysis

Growth analysis was carried out on plant material collected from the quadrat sampling. For samples taken at and before GS 31 soil was cleaned off the roots and the plant number of the whole sample recorded, before the roots were cut off and discarded. Growth analysis of the above ground plant material was identical for samples taken at all growth stages. Surface water on the above ground plant material was dried using paper towels and the fresh weight (g) of the whole sample was recorded to two decimal places. The sample was then divided into eight approximately equal parts, one of which was selected randomly and weighed. This sub-sample (SS1) was used for more detailed growth analysis. Two of the remaining seven parts were randomly selected as the second sub-sample (SS2) for dry weight (g) determination. The fresh weight of the SS2 was taken and it was oven dried at 80°C for 48 hours or until the samples had reached constant weight. The SS1 sub-sample was split into two categories of shoot; fertile shoots and dying/dead shoots (defined as when the newest expanding leaf had begun to turn yellow or no green material was present). The shoot number for each category was counted. Leaves were then removed from the shoots and placed in two categories: green leaves and non green leaves. Partly green leaves were dissected into green and non green parts. This gave four components; fertile stems, green leaf material, dead leaf material and dead/dying stems. The fresh weight of each was taken before the green area of the leaves and stems was measured using an image analyser (Delta-T Devices). The dry weight of each component was then determined using the method described above.

3.2.3 Harvest analysis

3.2.3.1 Pre-harvest analysis

Just prior to harvest ear number m^{-2} was determined using one of two methods. In the MT95 experiment the number of ears within a quadrat measuring 0.5 m x 0.5 m were counted. This was repeated five times in each plot and the mean taken. In the MT96 experiment the number of stems (with ears) were counted on either side of a 0.5m bar placed between the rows. Ear number m^{-2} for a plot was then calculated using the mean of five such samples and the row width.

Grab samples of approximately 100 stems with ears were taken from five randomly chosen areas in all plots by cutting the stems at ground level. These were processed in the laboratory to determine dry matter harvest index and ear and straw fresh weight. Fresh weight of the total sample was recorded, then all ears were cut off and counted, and straw and ear fresh weights recorded. A random 10 to 15% sub-sample of straw was selected, weighed to determine fresh weight, then oven dried to determine dry weight. All the ears were then threshed and the grain and chaff were collected. Fresh and dry weights of grain and chaff were measured.

3.2.3.2 Combining of plots and harvest analysis

Plots were combined by ADAS farm staff, under the following guidelines:
Prior to harvesting, tramlines were cut out, so that they did not form part of the harvested area and plot lengths were measured. For the harvest, one combine strip was taken through the centre of the combine area of the plot (to avoid plants influenced by the 'edge effect'). The width of the combine strip was accurately recorded; the area taken was approximately 10 m x 2.25 m. All fresh grain from each plot was weighed on the combine and a 1 kg sample of grain was taken for measurements of thousand grain weight, specific weight, Hagberg falling number and

grain moisture content. Plot yields were expressed as tonnes per hectare (t ha^{-1}) at 85% dry matter.

3.2.4 Lodging specific measurements

Lodging specific measurements were recorded on the ten plant samples.

3.2.4.1 Stem base component measurements

All stem base component measurements were done in the laboratory. For the purpose of this section the stem base consists of the basal internode, internode one and internode two only. Stem internodes were numbered according to the following methodology which remains consistent throughout the thesis. An internode which originated at or just below the ground surface and was more than ten millimetres in length was numbered as internode one. Subsequent internodes up the stem were then numbered two, three, four and five etc., with the final uppermost internode referred to as the peduncle. Basal internodes were defined as those which were ten millimetres or less in length and were generally situated at or just below ground level, always preceding internode one (Kirby *et al.*, 1994).

The width of the plant base at the soil surface was measured in millimetres. The stems of the plant were held in a similar position to that observed in the field for this measurement. The position on the stems at soil surface was identified by a change in stem colour from white to green, or by the point at which soil no longer adhered to the stems. This measurement was only taken for the MT95 experiment.

Main stems of each ten plant sample were identified using the method described in Kirby and Appleyard (1984), and their leaves removed. Measurements for the determination of stem failure moment and its components were then carried out on the basal internode, internode one and internode two of each main stem.

The length of each internode (mm) was measured from the mid-point of its adjacent nodes. Stem diameter (mm) was measured at the middle of each internode, using

digital callipers (Etalon). Tensile stem failure strength (g) was measured using a three-point bending test (Graham, 1983; Easson *et al.*, 1992). A vice was used to support the stem by adjusting the vice jaws to the exact length of each internode. The adjacent nodes of the internode were placed over the vice jaws and a pulling pressure was applied to the middle of the internode using a graduated Salter spring balance (1 kg x 10 g or 5 kg x 25 g). The hook of the spring balance was placed around the middle of the internode and pulled at an even rate until the stem buckled, at which point the force applied was recorded. Internodes were then cut at their centre point and digital callipers were used to measure the stem wall width (mm). For the MT96 experiment two measurements of stem wall width were taken on opposite sides of the stem, from which a mean was taken. Finally, stem failure moment (kPa) was calculated from internode length and stem failure strength, and stem failure yield stress (kPa) was calculated from the internode diameter, wall width and failure moment using basic structural theory (Baker, 1995).

3.2.4.2 Aerial component measurements

Laboratory measurements

To find the height at centre of gravity of the main shoot, the roots were cut off and the main shoot was balanced on a ruler (leaves and ear still attached) (Crook and Ennos, 1994). The distance from the point of balance to the stem base, was then defined as the height at centre of gravity (m) of the main stem. Height at centre of gravity was also measured for whole plants in the MT95 experiment. The same method was used, except that the roots were trimmed so as not to separate the shoots at the stem base, enabling all the shoots to be balanced together.

The area (cm^2) of ten main stem ears was measured using an image analyser (Delta-T Devices). Crop height (m) was measured from the soil surface to the top most leaf ligule or base of the ear collar (when emerged). Shoot number per plant was recorded

as was the number of internodes on each main stem. In the MT95 experiment ear fresh weight (g) was measured, using digital scales (Mettler).

In-field measurements

Natural frequency was measured by plant oscillation tests in the field. Firstly the main stem was identified and the surrounding stems were held away using a plastic cone placed over the main stem (narrow end first). The main stem was then pulled back (at the ear collar) ten centimetres from the vertical, and released. After release the number of 'significant' oscillations of the stem were counted and timed using a stopwatch. 'Significant' oscillations were defined as those where the stem oscillated straight back and forth in the same line as it was released. If the stem adopted circular oscillations i.e. oscillated laterally, the test was repeated. Natural frequency was calculated as the average time for one complete oscillation.

3.2.4.3 Root anchorage component measurements

Laboratory measurements

Seed depth (mm) was recorded at GS 30, by measuring from the seed case to the soil surface, defined as the junction between white and green tissue. In the MT95 experiment the presence or absence of a sub-crown internode between the seed and crown was also recorded.

The plant crown was defined as the origin of all tillers and adventitious roots (except the coleoptile tiller and its associated roots, should a sub-crown internode exist). Crown depth (mm) was measured from the base of the crown to the soil surface. In the MT95 experiment the width of the crown base (mm) was also measured.

The number of crown roots were counted on each plant. Crown roots were identified by their inherent rigidity and tendency for soil particles to stick to them due to their dense covering of root hairs (rhizosheath). This distinguished them from seminal

roots, which emerged from the seed, numbered six or less, were much less rigid and usually had no soil adhered to them (Ennos, 1991).

Crook and Ennos (1993) have described how the pattern of crown root development forms a 'root cone' (Figure 2.1), whose base is defined as the point along the crown root at which it is no longer sufficiently rigid (stiff) to provide anchorage. This section of crown root was identified by the point at which the root became more flexible, thinner and no longer had a dense covering of hairs on which soil was adhered. Root plate spread was defined as the width of the 'root cone' base (Figure 2.1). Both the maximum root plate spread (mm) and the root plate spread orientated at right angles to the maximum were measured. The second measurement was often the minimum root plate spread. These two measurements were averaged to gain the mean root plate spread. In the MT95 experiment the angle of root spread was also measured (Figure 2.1). As with root plate spread, a maximum and minimum angle were measured at 90° to each other. In the MT96 experiment the length of rigid root (mm) was measured (Figure 2.1). This measurement could be described as the length of the sloping side of the 'root cone'. The method by which the length of the rigid root was identified is given in the definition of the 'root cone' base. Once again two measurements were taken, similar to those described for root plate spread and angle of root spread.

In-field measurements

Root anchorage failure moment (Nm) was measured by plant displacement tests, using an overturning device, based on a torquemeter, designed by Ennos and Crook in 1994 (University of Manchester). The hand-held overturning device, was purpose built for use in the field, the measurement of force being based on a digital torquemeter (Mecmesin Ltd). The other appliances required for the device included; a tool chuck unit with a plastic cylinder housing, a rotation lever and displacement angle scale, ground spikes or metal base plate (for securing the device to the ground) and a rotation arm made of lightweight alloy. The method developed for measuring

anchorage failure moment was modified from the method of Crook and Ennos (1994) as follows:

1. Select one plant and cut off all shoots at a height of 50 mm above the ground.
2. Position the torquemeter, so the rotation arm rests against the cut stems.
3. Rotate the arm steadily, to 45° and measure the maximum force (Nm) during the rotation.

3.2.4.4 Soil measurements

The following soil measurements were taken as near to the roots as possible without damaging the root structure. These measurements were taken in conjunction with natural frequency measurements, anchorage failure moment measurements and lodging events.

Soil shear strength (kPa) was measured using a shear vane with a 19 mm blade diameter, at 25 mm and 50 mm depths below the soil surface. The shear vane was pushed into the soil to the required depth and the torque recorder rotated at a constant speed until the soil sheared. The torque required to shear the soil was then recorded (ADAS, 1982). Ten measurements of shear strength were taken at each depth, in each plot.

After each strength reading the soil adhering to the shear vane blades was collected and stored in sealed bags for soil moisture content (g g^{-1}) determination. Stones were removed by sieving before fresh weight determination. Soil was then oven dried at 100°C for 16 hours or until it reached constant weight and its dry weight recorded.

3.2.5 Disease assessment

Visual assessments for common symptoms of Eyespot (*Pseudocercosporella herpotrichoides*), Sharp eyespot (Rhizoctonia cerealis), Fusarium foot rot (*Fusarium*), and take-all (*Gaumannomyces graminis*) (Jones and Clifford, 1978) were carried out routinely whenever other measurements were taken. For the MT95

experiment these diseases were present at high levels so an assessment of stem based diseases was carried out at GS 87 on all treatments. These diseases were present only at very low levels in the other experiments, so full disease assessments were not carried out.

3.2.6 Environmental measurements

Rainfall (mm) and wind speed (m s^{-1}) were measured by an 'on site' automatic portable weather station (Delta-T Devices). During the lodging risk period of June to harvest, rainfall was recorded every 10 minutes, using a tipping bucket rain gauge, attached to the weather station. Wind speed was recorded every five seconds using a high resolution anemometer. Average wind speeds were calculated from these frequent readings, using software (Delta-T View). During the rest of the growing season, rainfall, wind speed, wind direction, temperature and humidity were recorded as daily means from data sampled at ten minute intervals. Daily sun hours and total daily radiation (kw m^{-2}) were measured a maximum of one kilometre from the field site, at the main ADAS Rosemaund weather station.

3.2.7 Lodging and leaning assessment

When lodging was observed assessments of its severity were made using the following indices:

Index 1 % crop area upright (crop leaning between 0° and 5° from the vertical).

Index 2 % crop area leaning (crop leaning between 5° and 45° from the vertical).

Index 3 % crop area lodged (crop lodged between 45° and 90° from the vertical).

Index 4 % crop area lodged flat.

Index 5 % crop area brackled (buckling of straw 1/4 or more up its length).

During lodging assessments, the dominant mechanism and point of failure was identified i.e. whether by stem failure or anchorage failure. Lodging assessments were made on areas of the plot which had not been previously sampled. A visual assessment of the percentage area of crop which was standing, leaning, lodged or lodged flat was made of the whole plot, including its edges, by walking around the

plot perimeter. For full details of the measurements taken in a lodged plot see Appendix 4.

3.2.8 Statistical analyses

Standard analysis of variance procedures for a split split plot design in randomised block with a two-way factorial in the sub-plots were used to calculate standard errors and significant differences between treatments. In the MT95 experiment, CHI squared tests were performed on the presence or absence of lodging in each plot due to the large number of plots which experienced no lodging. In the MT96 experiment, the percentage areas lodged per plot were transformed with a square root function to correct non-normally distributed data.

4. RESULTS: GENERAL CROP GROWTH

The following section provides a summary of weather conditions and crop growth over the 94-95 and 95-96 seasons. Spring soil mineral nitrogen levels (kg ha^{-1} N), crop establishment (plants m^{-2}), above ground dry weight (t ha^{-1}) green area index and shoot number (shoots m^{-2}) are used to describe and account for crop growth through the growing season. The treatments with the highest and lowest perceived lodging risks are used to illustrate the pattern of crop growth and the range of crop structures. The result of crop growth is described through grain yield (t ha^{-1}; at 85% dry matter), yield components and percentage area lodged at harvest. The final section of this chapter compares the weather and crop growth in the MT95 and MT96 experiments.

4.1 WEATHER

The 94-95 growing season was characterised by a very warm November and winter months, followed by average or slightly above average temperatures until harvest (Figure 4.1). Sun hours were similar to the long term mean apart from a very dull November and above average sun hours in March and April (Figure 4.2). September had twice its average rainfall and was followed by a wetter than average winter. Spring rainfall was below average with April receiving less than 50% of its normal rainfall. June and July were very dry, with 12 mm and 6 mm rain compared with long term averages of 50 mm and 48 mm respectively (Figure 4.3). Wind speeds were average or slightly below average for the summer months (Figure 4.4).

The 95-96 season had a warmer than average October followed by a colder than average winter. The rest of the growing season had temperatures similar to the long term mean, apart from May which was slightly colder (Figure 4.1). Average sun hours were experienced for the autumn and winter, followed by a very dull March which experienced less than half of its long term mean sun hours. The remainder of the growing season had sun hours similar to the long term mean, with June and July slightly above average (Figure 4.2). Average amounts of rain fell in autumn and winter followed by slightly above average rain in March and April. May to July had

below average rain, with July receiving less than 50 % of its long term mean (Figure 4.3). Mean wind speeds were slightly below average in June and July, but average in August (Figure 4.4).

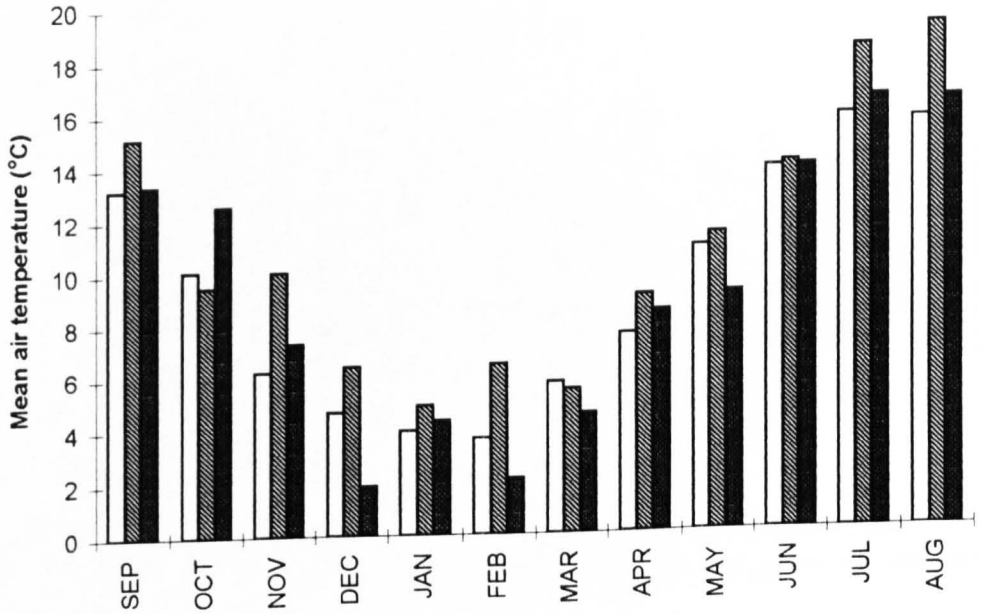

Figure 4.1 Monthly mean air temperatures at Rosemaund for the 30 year long term mean (open bars), 94-95 (hatched bars) and 95-96 (solid bars) growing seasons.

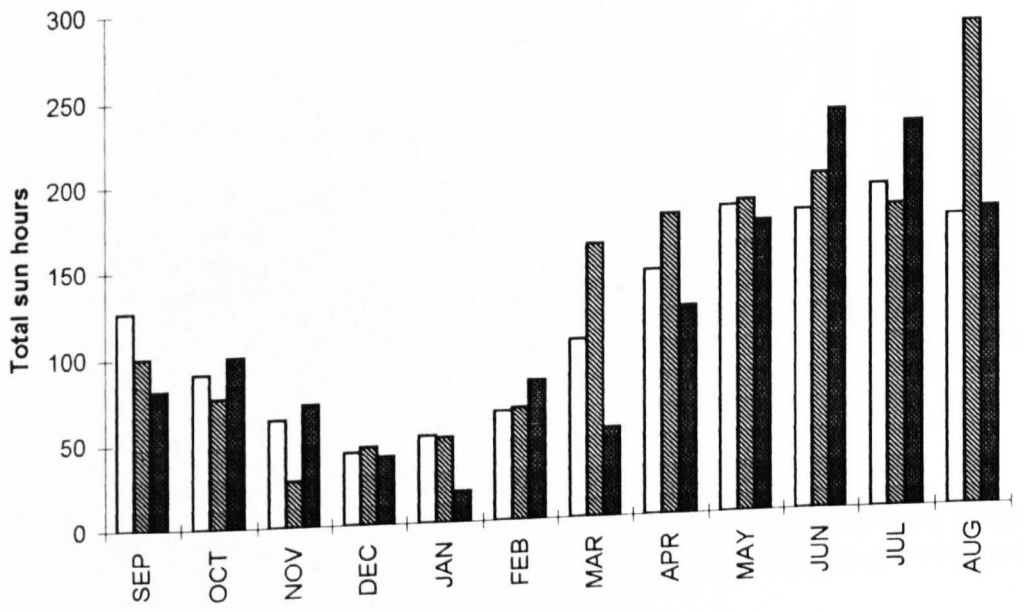

Figure 4.2 Monthly total sun hours at Rosemaund for the 30 year long term mean (open bars), 94-95 (hatched bars) and 95-96 (solid bars), growing seasons.

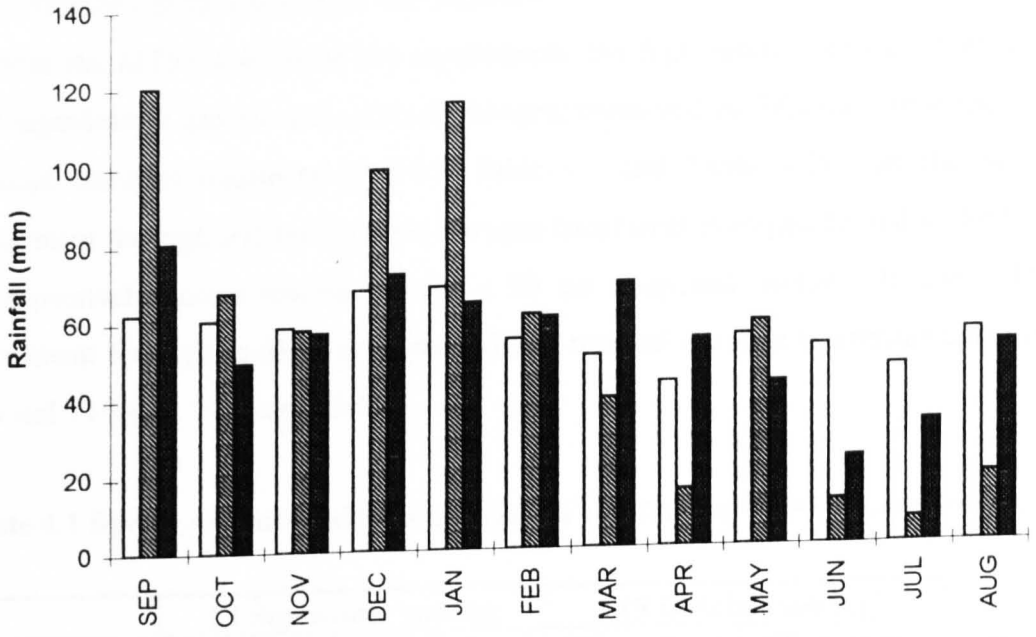

Figure 4.3 Monthly rainfall at Rosemaund for the 30 year long term mean (open bars), 94-95 (hatched bars) and 95-96 (solid bars) growing seasons.

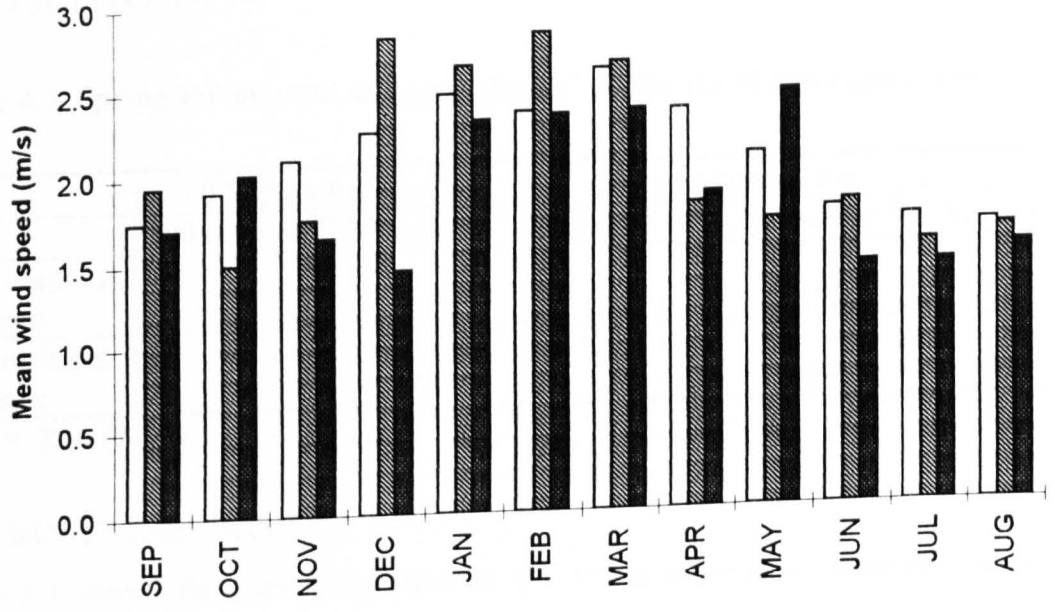

Figure 4.4 Monthly mean wind speed at Rosemaund for the 30 year long term mean (open bars), 94-95 (hatched bars) and 95-96 (solid bars) growing seasons.

4.2 SPRING SOIL MINERAL NITROGEN

In both the MT95 and the MT96 experiments, the high residual nitrogen treatment had significantly greater soil mineral nitrogen, measured in February, than the low residual nitrogen treatment ($P<0.01$; Table 4.1 and Table 4.2). In the MT95 experiment the high and low residual nitrogen treatments averaged 85 and 46 kg ha $^{-1}$ N respectively across treatments, for a 90 cm deep soil profile. In the MT96 experiment the high residual nitrogen and low residual nitrogen treatments averaged 116 and 71 kg ha $^{-1}$ N respectively.

Table 4.1 Spring soil mineral nitrogen (kg ha^{-1} N) for the MT95 experiment.

	23 September sowing		19 October sowing		
	500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}	Average
High residual nitrogen	78	79	87	96	**85**
Low residual nitrogen	41	38	47	59	**46**

SED = 16.1 (23 df)

Table 4.2 Spring soil mineral nitrogen (kg ha^{-1} N) for the MT96 experiment.

	20 September sowing		1 November sowing		
	500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}	Average
High residual nitrogen	94	111	130	132	**116**
Low residual nitrogen	65	65	77	77	**71**

SED = 22.0 (23 df)

4.3 CROP ESTABLISHMENT

Table 4.3 shows the plant population in the MT95 experiment measured on 4 November 1994. The high seed rate treatment had a significantly greater plant population than the low seed rate treatment ($P<0.001$). On average 420 plants m^{-2} were established for the high seed rate compared with only 226 for the low seed rate. This effect was influenced by sowing date as shown by an interaction between the sowing date and seed rate treatments ($P=0.086$). At high seed rate, the early sown

treatment had a significantly greater plant population than the late sown treatment. But, negligible differences in plant number were found between the sowing dates at low seed rate. No statistically significant differences in plant number were found for the sowing date and residual nitrogen treatments.

Table 4.4 shows the plant population in the MT96 experiment, which was measured on 26 October and 8 December 1995 for the early and late sown treatments respectively. There was a significantly greater plant population for the high seed rate (400 plants m^{-2}) compared with the low seed rate (192 plants m^{-2}; $P<0.001$). This effect was influenced by sowing date as shown by a statistically significant interaction between the sowing date and seed rate treatments ($P<0.05$). This interaction was similar to that found for MT95.

Table 4.3 Crop establishment (plants m^{-2}) for the MT95 experiment.

	23 September sowing		19 October sowing	
	500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High residual nitrogen	503	235	381	219
Low residual nitrogen	445	241	351	209
Average	**474**	**238**	**366**	**214**

SED = 35.7 (23 df)

Table 4.4 Crop establishment (plants m^{-2}) for the MT96 experiment.

	20 September sowing		1 November sowing	
	500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High residual nitrogen	459	201	327	183
Low residual nitrogen	475	197	334	187
Average	**467**	**199**	**331**	**185**

SED = 38.6 (23 df)

4.4 CROP GROWTH

A description of the growth and development of above ground dry matter, shoot number and green area index is given, using the treatments expected to have the highest and lowest lodging risks. This was done to demonstrate the diversity of crops which could be produced by different husbandry. The early sown, high seed rate, high residual nitrogen and nil lodging control treatment combination was deemed to have high lodging risk, and is shortened to 'high risk treatment'. The late sown, low seed rate, low residual nitrogen and nil lodging control treatment combination was deemed to have low lodging risk (shortened to 'low risk treatment'). For each data point, plus and minus one standard error of the mean (SEM) is described. The SEM is calculated from the analysis of variance carried out at each growth stage at which sampling was carried out. The number of degrees of freedom associated with the error bar at each sampling is given in Appendix 5, unless stated otherwise. This section is followed by an investigation of the effects of individual husbandry treatments on crop growth.

4.4.1 The MT95 experiment

4.4.1.1 Growth and development of the high and low risk treatments

Throughout the growing season the high and low risk treatments had similar patterns of growth and development for above ground dry weight (Figure 4.5), shoot number (Figure 4.6) and green area index (Figure 4.7). Development of the high risk treatment was ahead of the low risk treatment until the end of stem extension, after which developmental dates were similar. At early growth stages (GS 30 and GS 31) no statistically significant differences were found between the high and low risk treatments for above ground dry weight, shoot number or green area index. At GS 33 and 39 the high risk treatment generally had a greater above ground dry weight, shoot number and green area index than the low risk treatment. These differences were statistically significant for above ground dry weight at GS 33 and GS 39 and for green area index at GS 33 and GS 39 ($P<0.05$). At GS 39 the high risk treatment had a green area index of 6.6 compared with 4.9. At harvest the high risk treatment had

significantly more shoots, 584 compared with 497 shoots m^{-2}, but a much smaller above ground dry matter, 15.2 t ha^{-1} and 18.5 t ha^{-1} dry weight (Figure 4.5).

Analysis of the above ground dry weights at harvest show that the high risk treatment had an unusually low dry weight. For example, another perceived high lodging risk treatment of early sown, high seed rate, *low* residual nitrogen and nil lodging control, had accumulated about two tonnes more dry weight by harvest and was similar in size to the dry weight of the low lodging risk treatment. The treatment combination with the highest perceived lodging risk resulted in 64 percent area lodged at harvest (Figure 4.8) compared with an absence of lodging for the low risk treatment. It should be noted that all lodging was stem lodging and apart from the high risk treatment, the lodging encountered was slight and mainly occurred late in the growing season from GS 77 onwards (Figure 4.8). The severe lodging which occurred during grain filling in the high risk treatment may have curtailed growth. This could account for its small above ground dry weight at harvest compared with other treatments.

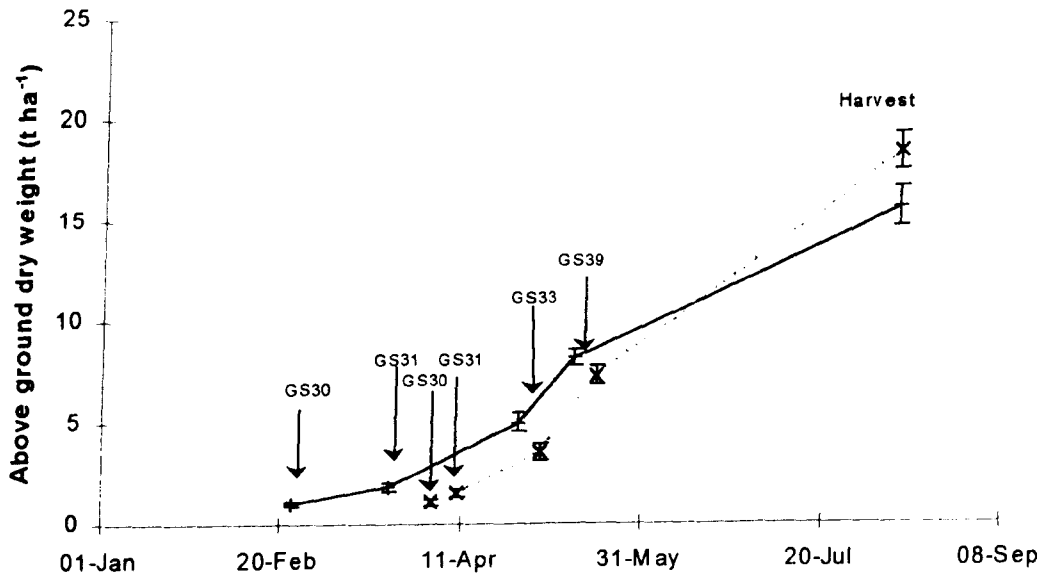

Figure 4.5 The development of above ground dry weight in the MT95 experiment season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (8-56 df, see Appendix 5).

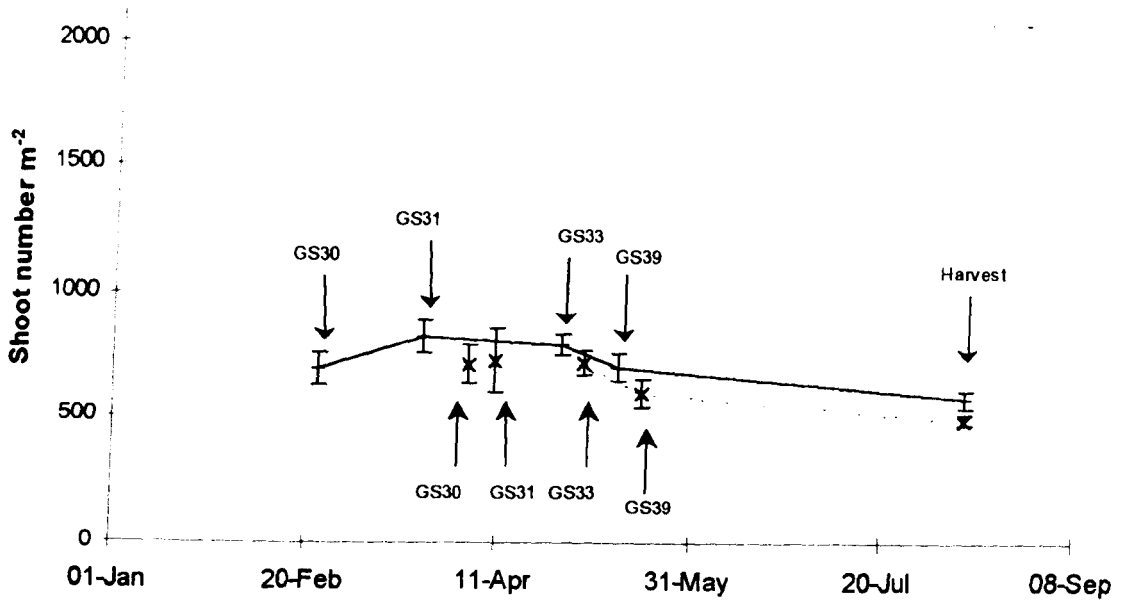

Figure 4.6 The development of shoot number in the MT95 experiment season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (8-56 df, see Appendix 5).

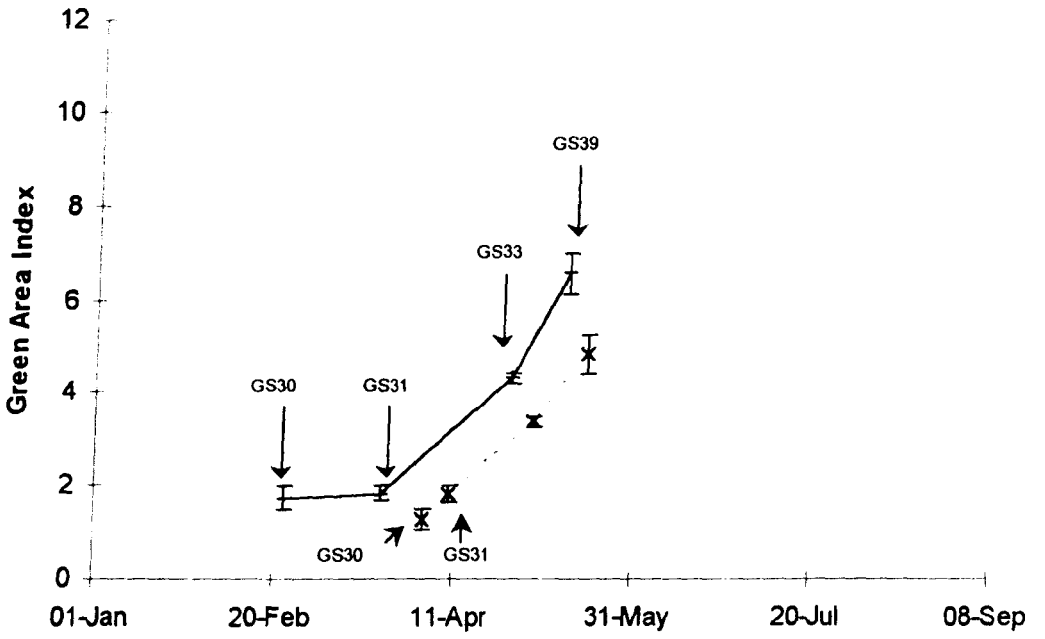

Figure 4.7 The development of green area index in the MT95 experiment season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (8-24 df, see Appendix 5).

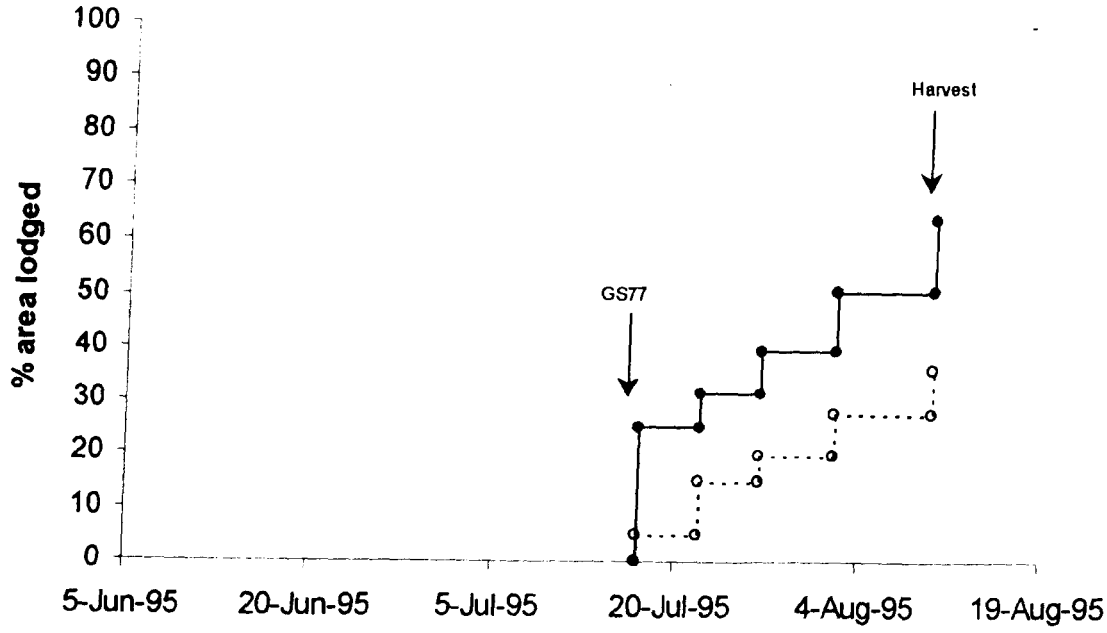

Figure 4.8 The progression of lodging (index 2, 3, 4 and 5 inclusive) in the 94-95 season for the treatments which were early sown at high seed rate, with no PGR on high soil residual N (—•—) and low soil residual N (--o--).

4.4.1.2 The influence of husbandry on crop growth and lodging

To act as a general point of reference for this section and to illustrate the influence of different husbandry combinations on crop growth, green area index at GS 39, above ground dry weight, shoot number, grain yield and frequency of lodged plots at harvest are shown in Tables 4.5 to 4.9.

Sowing date

Generally no statistically significant differences were found between the two sowing date treatments throughout the growing season (GS 30 to harvest) for above ground dry weight, shoot number, green area index or for grain yield (Table 4.8). However, at GS 33 and GS 39 the high seed rate treatment which was sown early had a significantly greater green area index and above ground dry weight than the other sowing date/seed rate combinations ($P<0.05$). This may explain why the early sown treatment had significantly more lodging than the late sown treatment at harvest

($P<0.05$), with 19 out of 48 plots experiencing lodging compared with only 3 out of 48 (Table 4.9).

Seed rate

In general, high seed rates had a greater above ground dry weight, shoot number and green area index at early growth stages. High seed rate was associated with greater above ground dry weight at GS 31, GS 33 and GS 39 ($P<0.05$), more shoots per metre squared at GS 30 ($P<0.01$) and GS 31 ($P<0.05$), and a larger green area index at GS 30, 31, 33 and 39 ($P<0.05$), compared with low seed rate. These effects were often influenced by an interaction between sowing date and seed rate. This interaction was observed for above ground dry weight at GS 33 and GS 39 ($P<0.05$), for shoot number at GS 30 and GS 31 ($P<0.05$) and for green area index at GS 33 ($P<0.05$). The level of significance of the interaction was nearly always equal to that of the main seed rate effect, and was therefore of equal certainty. An analysis of the factorial tables revealed that these interactions were always due to large differences due to seed rate with early sowing and small differences due to seed rate with late sowing.

At harvest no statistically significant differences were found due to seed rate for above ground dry weight (Table 4.6), shoot number (Table 4.7), grain yield (Table 4.8), specific grain weight or thousand grain weight. However, high seed rate significantly increased the number of plots which experienced lodging ($P<0.05$). High seed rate had 18 out of 48 plots with lodging compared to 4 out of 48 plots for low seed rate (Table 4.9). It appears that seed rate caused differences in crop growth during stem extension, particularly for the early sown crops and these appear to be linked with the differences in lodging.

Residual nitrogen

High residual nitrogen increased above ground dry weight, shoot number and green area index during early stem extension (GS 30 and GS 31) compared to low residual nitrogen ($P<0.05$). This effect continued for green area index until measurements of

this character ceased at GS 39 (Table 4.5). The influence of residual nitrogen on above ground dry weight and shoot number decreased as the season progressed and any effects were complicated by statistically significant high order interactions with the seed rate and lodging control treatments. At harvest high residual nitrogen caused a small, but significant ($P<0.01$) increase in shoot number, from 503 to 520 shoots m^{-2} (Table 4.7). However, no statistically significant differences were found for the above ground dry weight, grain yield, specific weight or frequency of lodging at harvest.

Lodging controls

The PGRs 5C Cycocel and Terpal had little or no effect on crop growth. Above ground biomass was significantly reduced by 5C Cycocel at GS 39 ($P<0.05$), but there was no significant difference at harvest. 5C Cycocel did not increase shoot number, as found by other studies (Green, 1986). Grain yield was not affected by PGRs. Out of 24 plots, lodging was experienced in nine plots for the nil lodging control treatment, five plots for 5C Cycocel and one plot for 5C Cycocel followed by Terpal.

At harvest, Canopy Management significantly reduced above ground dry weight ($P<0.001$), shoot number from 527 to 468 shoots m^{-2} ($P<0.05$) and grain yield from 9.5 to 9.2 t ha^{-1} ($P<0.001$). This treatment increased specific grain weight from 81.7 to 83.0 kg hl^{-1} ($P<0.001$) and increased thousand grain weight from 42.6 to 47.0g ($P<0.001$). It may be that dry conditions reduced uptake of the late nitrogen application, resulting in a smaller shoot number and smaller above ground dry weight. A similar number of plots lodged with and without Canopy Management, despite its smaller biomass. This may be due to the greater ear weight caused by this treatment.

In summary, statistically significant differences in crop growth were generated by the seed rate and residual nitrogen treatments between GS 30 and GS 39, such that above ground dry weight, shoot number and green area index were increased by high seed rate and high residual nitrogen. It was also observed that seed rate had its greatest effect in association with early sowing. By harvest these effects were less certain or not detectable, yet significant differences in the number of lodged plots were

observed. It may be that variation in early season growth is linked with some of these differences in lodging severity. The PGR controls caused the expected reduction in area lodged without affecting crop biomass and shoot number. These factors must exert their influence by affecting other crop characters such as crop height, although changes in other characters such as anchorage strength and stem strength cannot be ruled out.

Table 4.5 Green area index at GS39 for the MT95 experiment

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High residual	Nil spring lodging control	6.6	5.2	5.7	5.4
soil nitrogen	5C Cycocel (PGR)	6.9	5.3	5.5	5.4
Low residual	Nil spring lodging control	5.8	5.0	4.8	4.9
soil nitrogen	5C Cycocel (PGR)	5.7	4.6	5.9	5.1

SED = 0.73 (23 df)

Table 4.6 Above ground dry weight (t ha^{-1})at harvest for the MT95 experiment

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	15.8	17.4	17.1	17.9
soil	5C Cycocel (PGR)	16.5	17.2	17.6	18.1
residual	5C Cycocel + Terpal (PGR)	18.4	17.3	17.8	18.2
nitrogen	Reduced spring nitrogen	16.1	15.6	16.7	16.3
Low	Nil spring lodging control	17.7	17.5	17.9	18.5
soil	5C Cycocel (PGR)	17.3	16.9	16.9	17.2
residual	5C Cycocel + Terpal (PGR)	17.2	17.1	17.3	17.3
nitrogen	Reduced spring nitrogen	16.1	15.2	15.1	15.5

SED = 0.94 (56 df)

Table 4.7 Shoot number m^{-2} at harvest for the MT95 experiment

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	584	536	539	450
soil	5C Cycocel (PGR)	553	497	533	536
residual	5C Cycocel + Terpal (PGR)	540	496	576	544
nitrogen	Reduced spring nitrogen	492	442	481	526
Low	Nil spring lodging control	526	515	539	528
soil	5C Cycocel (PGR)	522	512	510	499
residual	5C Cycocel + Terpal (PGR)	554	461	545	534
nitrogen	Reduced spring nitrogen	477	431	450	442

SED = 26.5 (56 df)

Table 4.8 Grain yield (t ha^{-1}; at 85% dry matter) for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	8.6	9.3	9.3	10.1
soil	5C Cycocel (PGR)	9.2	9.3	10.0	9.9
residual	5C Cycocel + Terpal (PGR)	9.6	10.1	10.3	10.1
nitrogen	Reduced spring nitrogen	9.2	9.3	10.0	9.9
Low	Nil spring lodging control	9.6	9.6	9.9	10.0
soil	5C Cycocel (PGR)	9.6	9.4	9.7	9.7
residual	5C Cycocel + Terpal (PGR)	9.2	9.7	10.1	10.1
nitrogen	Reduced spring nitrogen	9.6	9.4	9.7	9.7

SED = 0.47 (56 df)

Table 4.9 Lodging at harvest for the MT95 experiment, scored as the number of the three replicate plots per treatment which experienced lodging. (Followed by the mean percentage area lodged at harvest for each treatment).

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	3 (64)	1 (2)	0 (0)	0 (0)
soil	5C Cycocel (PGR)	3 (7)	0 (0)	0 (0)	0 (0)
residual	5C Cycocel + Terpal (PGR)	1 (5)	0 (0)	0 (0)	0 (0)
nitrogen	Reduced spring nitrogen	2 (40)	0 (0)	1 (0)	0 (0)
Low	Nil spring lodging control	3 (36)	1 (3)	1 (0)	0 (0)
soil	5C Cycocel (PGR)	1 (8)	0 (0)	0 (0)	1 (0)
residual	5C Cycocel + Terpal (PGR)	0 (0)	0 (0)	0 (0)	0 (0)
nitrogen	Reduced spring nitrogen	3 (8)	1 (0)	0 (0)	0 (0)

CHI-squared tests on presence or absence of lodging
CHI square = 59.8 (30 df)

4.4.2 The MT96 experiment

4.4.2.1 Growth and development of the high and low risk treatments

Above ground dry weight and green area index had similar patterns of growth and development throughout the growing season for the high and low risk treatments, but displaced in time (Figure 4.9 and Figure 4.10). The pattern of the growth and development for shoot number was different (Figure 4.11). The maximum shoot number of the high risk treatment was reached before the beginning of stem extension in December, after which it declined to its smallest value at harvest. For the low risk treatment the maximum shoot number was reached in April, at GS 31, after which it declined to its smallest value at harvest. Development of the high risk treatment was always ahead of the low risk treatment, but this difference decreased considerably towards harvest. The high risk treatment had a significantly greater above ground dry weight (Figure 4.9), shoot number (Figure 4.11) and green area index (Figure 4.10) over winter and at GS 30, 31, 33 and GS 39 ($P<0.05$).

At harvest the high risk treatment had less above ground dry weight and a similar shoot number compared with the low risk treatments (Figure 4.9 and Figure 4.11). Analysis of the above ground dry matter and shoot number data at harvest showed that other perceived high lodging risk treatments had a higher above ground dry weight and shoot number than the low risk treatment. This is illustrated by a comparison of another high risk treatment (early sowing, high seed rate and *low* residual nitrogen) with the low lodging risk treatment. This high risk treatment had an above ground dry weight of 18.4 t ha^{-1} and shoot number of 789 shoots m^{-2} compared with 16.3 t ha^{-1} and 672 shoots m^{-2} for the low risk treatment. Thus, at harvest the high lodging risk treatments generally had a greater above ground dry weight and shoot number than the low lodging risk treatments. There was a large variation in the per cent area lodged, with 93 % in the high risk treatment and only 8 % in the low risk treatment. Almost all of the lodging observed was root lodging which occurred early (GS 58 onwards) and continued to occur sporadically until harvest (Figure 4.12). Similar to observations in the MT95 experiment the severe early lodging which occurred in the high lodging risk treatment may have curtailed growth. This could account for its small above ground dry weight and shoot number at harvest compared with other high risk treatments which lodged less severely.

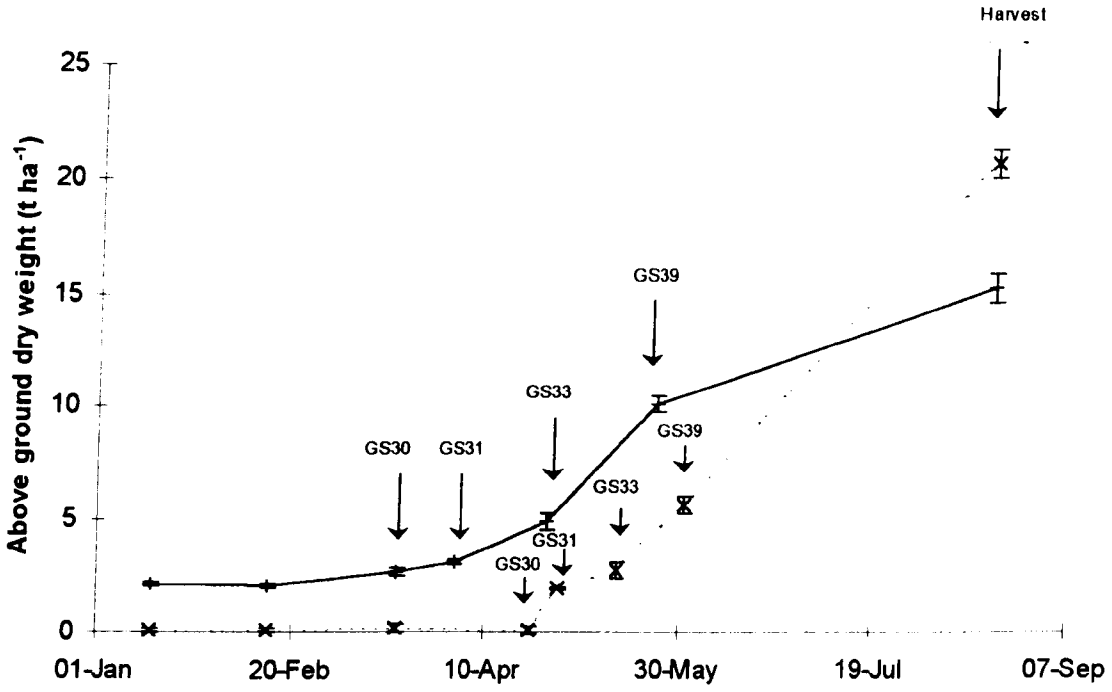

Figure 4.9 The development of above ground dry weight in the MT96 experiment season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (8-56 df, see Appendix 5).

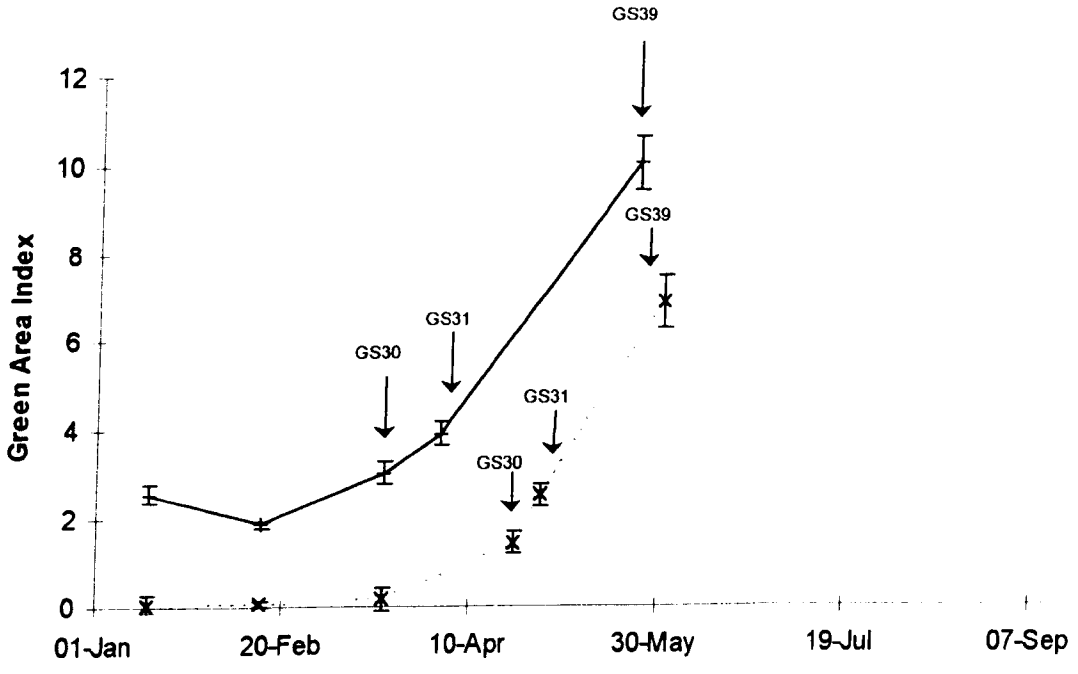

Figure 4.10 The development of green area index in the MT96 experiment season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (8-24 df, see Appendix 5).

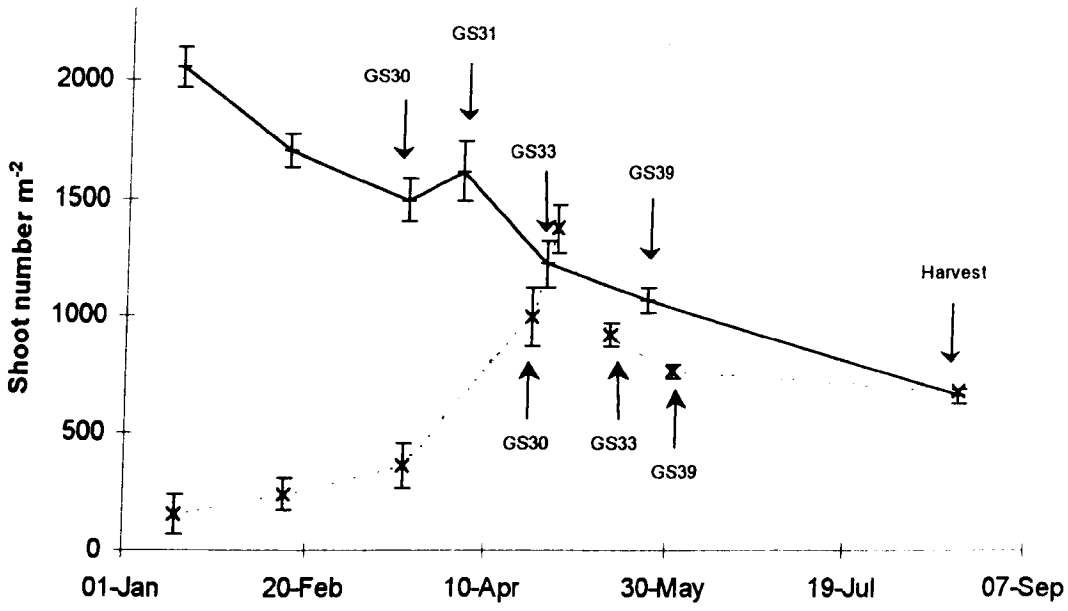

Figure 4.11 The development of shoot number in the MT96 experiment season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (8-56 df, see Appendix 5).

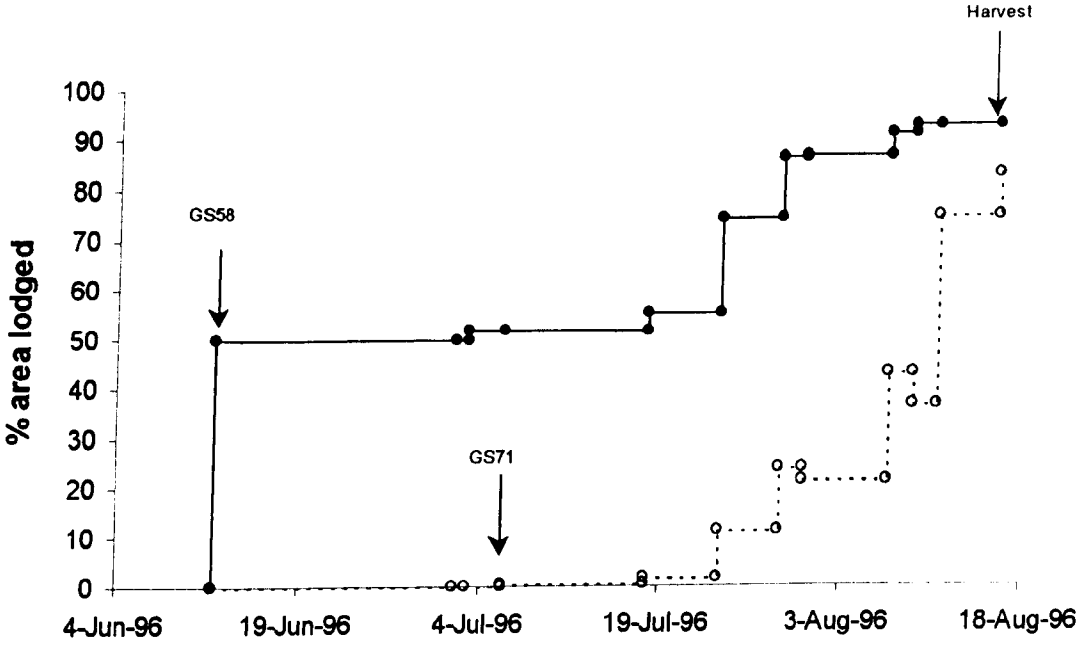

Figure 4.12 The progression of lodging in the 95-96 season for the treatments which were early sown at high seed rate, with no PGR on high soil residual N (—•—) and low soil residual N (--o--).

4.4.2.2 The influence of husbandry on crop growth and lodging

To act as a general point of reference for this section and to illustrate the influence of different husbandry combinations on crop growth: green area index at GS 39, above ground dry weight, shoot number, grain yield and frequency of lodged plots at harvest are shown in Tables 4.10 to 4.14.

Sowing date

Over winter and throughout the spring at GS 30, 31, 33 and 39, the early sown treatment had a greater above ground dry weight, green area index and shoot number than the late sown treatment ($P<0.05$). The differences in above ground dry weight (Table 4.11) and shoot number (Table 4.10) were maintained until harvest, when early sowing produced an average above ground dry weight and shoot number of 17.7 t ha^{-1} and 774 shoots m^{-2} compared with 15.7 t ha^{-1} and 691 shoots m^{-2} for late sowing. Early sown crops also and a greater percentage area lodged per plot ($P<0.001$; Tabloe 4.14). The early sown plots had on average 45 % area lodged compared with only 9 % for the late sown plots. Early sowing caused a slight reduction in grain yield from 9.85 to 9.56 t ha^{-1} ($P=0.093$; Table 4.13). The yield reducing effect of severe lodging probably caused this. However, the effect on grain yield was complicated by a statistically significant interaction between the sowing date, residual nitrogen and lodging control treatments ($P<0.05$). The interaction probably resulted from the early sown, high residual nitrogen and nil lodging control treatment having a considerably lower grain yield (8.1 t ha^{-1}) than the other treatments, as a result of severe lodging. The early sown treatment also had a lower dry matter harvest index of 0.46, compared with 0.54 for the late sown treatment ($P<0.05$).

Seed rate

During winter, high seed rate significantly increased the above ground dry weight, green area index and shoot number compared with the low seed rate ($P<0.05$) in the early sown treatments. At GS 30, 31 and 33, these differences were expressed for both early and late sown treatments and were significant ($P<0.05$), apart from shoot number at GS 31. At GS 39 only shoot number showed large differences between

seed rates (P=0.054). By harvest no statistically significant differences were found for above ground dry weight (Table 4.11) and shoot number (Table 4.12) due to seed rate. Despite this, high seed rate plots had on average 36 % area lodged compared with 18 % area lodged (P<0.05). This effect was influenced by a significant interaction between the sowing date, seed rate and lodging control treatments (P<0.01) (Table 4.14). This was because the lodging control treatments had a small effect on the area lodged for the highest and lowest lodging risk treatments, such as early sowing at high seed rate compared with late sowing at low seed rate. However, lodging control treatments had a much greater effect on the treatment combinations of intermediate lodging risk. High seed rate significantly decreased thousand grain weight (P<0.01), but had no statistically significant effect on grain yield (Table 4.13), specific grain weight or dry matter harvest index.

Residual nitrogen

Throughout the winter months high residual nitrogen increased above ground dry weight, shoot number and green area index (P<0.05) in the early sown treatments. This effect was maintained for above ground dry weight and green area index at GS 30, GS 31 and GS 33 for both sowing dates (P<0.05). High residual nitrogen also increased shoot number at GS 31 (P=0.081) and GS 33 (P=0.083). However, at GS 39 and harvest, high residual nitrogen had ceased to increase crop growth (Table 4.11, Table 4.10 and Table 4.12). At harvest, high residual nitrogen was associated with a greater per cent area lodged (37 %) compared with low residual nitrogen (17 %) (P<0.001; Table 4.14). High residual nitrogen was also associated with a decrease in the above ground dry weight (P<0.05; Table 4.10) and decreased grain yield from 9.86 to 9.54 t ha^{-1} (P<0.001; Table 4.13). These effects may have been due to lodging reducing late crop growth in the high residual nitrogen crops. The residual nitrogen treatments had no statistically significant effects on specific grain weight or dry matter harvest index.

Lodging controls

The PGRs 5C Cycocel and Terpal did not affect above ground dry weight, shoot number or green area index. The percent area lodged was significantly decreased from 53 % to 26 % by 5C Cycocel and further to 9 % by 5C Cycocel with Terpal ($P<0.001$; (Table 4.14). Canopy Management reduced the percent area lodged from 53 % to 21 % ($P<0.001$; Table 4.14). However, this treatment also significantly reduced the harvest above ground dry weight ($P<0.001$; Table 4.11), shoot number ($P<0.001$; Table 4.12) and grain yield by about 0.5 t ha^{-1} ($P<0.001$; Table 4.13). The Canopy Management treatment had a greater thousand grain weight ($P<0.001$). This indicates that at grain filling there was more than enough assimilate to fill the grain sites, but there may not have been adequate grain sites to fill. This could be due to either the formation of too few ears or too few fertile grain sites per ear. This may have been because the Canopy Management treatment received about 150 kg ha^{-1} N less than the conventional treatments. Despite this low nitrogen application Canopy Management far exceeded its target green area index of five in many cases.

In summary, the extreme high and low risk treatments had large differences in crop growth throughout the season and differed substantially in the lodging they experienced. The sowing date, seed rate and residual nitrogen treatments generated large differences in crop growth, such that above ground dry weight, shoot number and green area index were increased by the early sown, high seed rate and high residual nitrogen treatments. These differences were maintained until harvest for the sowing date treatments, but the seed rate and residual nitrogen treatment differences had reduced or disappeared by harvest. Nevertheless, statistically significant effects were found between the per cent area lodged for all the main treatments. It appears that in some cases husbandry can cause differences in crop size which are maintained all season which then relate to the severity of lodging. However, in other cases early season growth differences have reduced or disappeared by the time lodging occurs. This suggests that early season growth patterns are linked with lodging later in the season, as found in the MT95 experiment.

Table 4.10 GAI at GS 39 for the MT96 experiment

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High residual	Nil spring lodging control	10.1	10.8	7.5	7.4
soil nitrogen	5C Cycocel (PGR)	9.1	10.0	7.9	7.1
Low residual	Nil spring lodging control	11.1	10.5	7.8	7.0
soil nitrogen	5C Cycocel (PGR)	9.8	10.0	8.2	6.6

SED = 0.86 (23 df)

Table 4.11 Above ground dry weight (t ha^{-1}) at harvest for the MT96 experiment

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	15.2	17.5	16.1	15.9
soil	5C Cycocel (PGR)	18.6	18.3	16.1	16.2
residual	5C Cycocel + Terpal (PGR)	18.1	17.3	16.0	14.9
nitrogen	Reduced spring nitrogen	16.6	17.7	13.8	14.5
Low	Nil spring lodging control	18.4	20.7	16.3	16.3
soil	5C Cycocel (PGR)	17.5	18.5	16.3	15.5
residual	5C Cycocel + Terpal (PGR)	18.1	18.2	16.3	15.9
nitrogen	Reduced spring nitrogen	15.8	16.5	16.4	14.5

SED = 0.98 (56 df)

Table 4.12 Shoot number m^{-2} at harvest for the MT96 experiment

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	663	751	691	713
soil	5C Cycocel (PGR)	782	806	723	684
residual	5C Cycocel + Terpal (PGR)	848	812	766	736
nitrogen	Reduced spring nitrogen	768	757	657	633
Low	Nil spring lodging control	789	733	712	672
soil	5C Cycocel (PGR)	838	800	680	658
residual	5C Cycocel + Terpal (PGR)	824	775	711	682
nitrogen	Reduced spring nitrogen	724	706	688	650

SED = 44.0 (56 df)

Table 4.13 Grain yield (t ha^{-1}; at 85% dry matter) for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	8.1	9.4	10.1	10.1
soil	5C Cycocel (PGR)	10.1	10.0	9.8	10.1
residual	5C Cycocel + Terpal (PGR)	9.5	9.7	9.9	9.5
nitrogen	Reduced spring nitrogen	9.1	9.3	9.2	9.0
Low	Nil spring lodging control	9.7	10.3	10.1	10.3
soil	5C Cycocel (PGR)	10.4	10.2	10.0	9.9
residual	5C Cycocel + Terpal (PGR)	9.8	10	10.1	10.1
nitrogen	Reduced spring nitrogen	8.7	8.9	9.9	9.5

SED = 0.36 (56 df)

Table 4.14 Square root transformation of the mean percentage area lodged at harvest for the MT96 lodging experiment. (Followed by the mean percentage area lodged).

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	9.7 (93)	9.3 (87)	7.0 (54)	3.7 (15)
soil	5C Cycocel (PGR)	9.4 (88)	7.0 (52)	2.6 (7)	2.2 (4)
residual	5C Cycocel + Terpal (PGR)	6.4 (45)	3.9 (15)	1 (1)	1.2 (1)
nitrogen	Reduced spring nitrogen	8.9 (80)	6.8 (47)	0.7 (0)	0.9 (0)
Low	Nil spring lodging control	9.2 (83)	6.2 (40)	6.4 (44)	2.7 (8)
soil	5C Cycocel (PGR)	6.3 (40)	2.8 (9)	1.9 (3)	1.7 (3)
residual	5C Cycocel + Terpal (PGR)	2.8 (7)	1.8 (3)	1.2 (1)	0.7 (0)
nitrogen	Reduced spring nitrogen	4.8 (23)	2.2 (7)	2 (4)	0.9 (1)

SED = 0.97 (56 df)

4.5 COMPARISON OF THE MT95 AND MT96 EXPERIMENTS

4.5.1 Crop establishment, soil residual nitrogen and weather

On average about 400 plants m^{-2} were established for high seed rate and 200 for low seed rate in both experiments. However, plant establishment was slightly poorer in the MT96 experiment, with the late sown high seed rate combination having the poorest establishment. Soil mineral nitrogen levels were about 30 kg ha^{-1} greater in the MT96 experiment compared with the MT95 experiment. This could be one reason why growth in the MT96 experiment was greater. Both experiments had a difference between the high and low residual nitrogen treatments of about 40 kg ha^{-1} N.

The most striking weather aspects of the 94-95 growing season included a warm autumn and winter followed by a very dry April, June and July. The combined June and July rainfall was less than 20 % of the long term mean. The 95-96 growing season was typified by a cool May followed by low rainfall in June and July which was less than 50 % of the long term mean. The low summer rainfall in 1995 and 1996 would probably be expected to give little lodging according to conventional wisdom.

The larger soil mineral nitrogen and cool May in 1996 may have increased tiller survival by increasing assimilate supply to the shoots in relation to developmental rate. This may help account for the high shoot numbers and greater lodging in this year.

4.5.2 Crop growth and development

An assessment of crop growth in the 94-95 and 95-96 seasons can be gained by comparison with a 'bench mark' Mercia crop, as described in the 'Wheat Growth Guide' (Sylvester-Bradley *et al.*, 1998a). Information for this guide was compiled from data on the growth and development of Mercia from 18 site seasons, of which the early sown, high seed rate, high residual nitrogen, with 5C Cycocel and Terpal treatment of the MT95 experiment formed one site season. Growth data from this treatment and from an identical treatment in the MT96 experiment have been compared with the 'bench mark' wheat crop in Table 4.16.

Table 4.16 Comparison of crop growth and development from the MT95 and MT96 experiments with the 'bench mark' wheat crop, described in the 'Wheat Growth Guide' (Sylvester-Bradley *et al.*, 1998a).

	Bench mark crop	94-95	95-96
Sowing date	7 October	23 September	20 September
Spring plant number m^{-2}	302	470	449
GS 31 date	30 April	22 March	2 April
GS 31 green area index	1.9	1.7	3.0
GS 31 dry weight t ha^{-1}	1.6	1.0	2.7
maximum shoot number m^{-2}	978	829	1989
GS 39 date	23 May	12 May	24 May
GS 39 green area index	5.9	6.6	10.1
GS 39 dry weight t ha^{-1}	6.6	8.2	10.1
Harvest ear number m^{-2}	604	540	848
Harvest grain number per ear	33	43	31
Harvest thousand grain weight	46	41	36
Harvest dry weight t ha^{-1}	17.4	17.2	18.1
Harvest grain yield t ha^{-1}	9.1	9.6	9.8

It must first be noted that the crops of the MT95 and MT96 experiments had about 50% more plants established than the 'bench mark' wheat crop. This may be expected to increase growth at early stages of development. Early growth was smaller in the 94-95 season and much greater in the 95-96 season in comparison with the 'bench mark' wheat crop. Growth in the 94-95 season later caught up that of the bench mark wheat crop to finish with a similar above ground dry weight and a greater grain yield, which resulted from a large number of grains per ear. The Crop growth in the 95-96 season was considerably greater than that of the 'bench mark' wheat crop throughout the season and finished with a greater above ground dry weight, ear number and grain yield. It appears that crop growth in the 94-95 season was about 'average' despite a slow start. However, all aspects of crop growth throughout the 95-96 season must be considered very large.

4.5.3 The influence of husbandry

The MT96 experiment had much greater differences in crop growth between the high and low lodging risk treatments than the MT95 experiment. By harvest, differences in growth between the high and low risk treatments were still large in the MT96 experiment, but had become smaller in the MT95 experiment. The lodging observed in the high risk treatment was more severe in MT96 than in MT95. Lodging in the high risk treatment is thought to have reduced late growth, causing a reduction in above ground dry weight and grain yield in both experiments.

Early sowing increased lodging in both experiments, however only small differences in crop growth were observed during the early part of the MT95 experiment compared with large differences throughout the MT96 experiment. The effects of seed rate and residual nitrogen on lodging were slightly weaker than the sowing date effects. High seed rate increased lodging in both experiments and high residual nitrogen increased lodging in the MT96 experiment. In general, both treatments increased crop growth between GS 30 and GS 39, but caused little or no differences in above ground dry weight or shoot number at harvest in either experiment. Importantly, it was found

that lodging could be considerably reduced by particular combinations of sowing date, seed rate and residual nitrogen without remedial controls and without reducing grain yield. In fact the treatments with a perceived high yield potential had the lowest yields due to severe lodging.

PGRs reduced lodging in both experiments (although not significantly in MT95). However, they had no consistent effect on crop growth in terms of above ground dry weight, shoot number and green area index. Canopy Management reduced lodging in the MT96 experiment, possibly due to it's smaller above ground dry weight and shoot number. This treatment was also associated with reduced grain yield, although this may have been peculiar to these experiments since other research has shown little or no yield loss with this management practice (Sylvester-Bradley *et al.*, 1997). In the MT96 experiment, some Canopy Management treatments reduced lodging whilst causing little or no yield loss.

4.5.4 Conclusions

In both experiments the summer weather conditions were not conducive to lodging, yet the MT96 experiment experienced considerably more lodging. It would appear that greater crop growth, in terms of above ground dry weight, shoot number and green area index, brought about by the different environmental conditions of the MT96 experimental season may have increased lodging risk. This, coupled with slightly wetter conditions in the summer of 1996 probably explain why considerable amounts of root lodging were experienced in MT96 compared with small amounts of stem lodging in MT95.

The experiments have shown that husbandry has a very large influence on crop structure and lodging. This is notwithstanding that the early differences in crop structure have often diminished or disappeared when lodging occurs. It appears that early differences in crop growth may be indirectly and subtly linked with differences in lodging severity later in the season. It will be important to elucidate the mechanism

by which these early season growth differences might affect lodging if there is to be a full understanding of how husbandry affects lodging.

Baker *et al.* (Appendix 1) have shown that the occurrence of stem or root lodging is determined by an interaction of the weather with the plant and soil through leverage force, stem strength and anchorage strength. These components were shown to be dependent on a relatively small number of plant characters, which include stem base diameter, stem wall width, stem failure yield stress, natural frequency, height at centre of gravity, shoot number per plant, root plate spread and structural rooting depth. It appears likely that early season crop growth affects lodging indirectly by influencing the growth of these lodging-associated plant characters. The next chapter uses information from the MT95, MT96 and VT95 experiments to investigate the development and growth of these plant characters and how they are influenced by season, site, husbandry and genotype.

5. PLANT CHARACTERS ASSOCIATED WITH LODGING

This chapter reports the influence of season, husbandry and variety on the growth and development of the plant characters associated with lodging, using data from the MT95, MT96 and VT95 experiments. Subsection 5.1 investigates the plant characters which determine stem failure moment, 5.2 investigates the plant characters which determine base bending moment of a single shoot, 5.3 investigates shoot number per plant and 5.4 investigates plant characters associated with anchorage failure moment. Subsection 5.5 summarises the findings of this chapter and assesses the value of developing a prediction scheme for each lodging-associated plant character.

Within each subsection, a description of the development of each plant character is given for the whole growing season, using the treatment combinations with the high and low lodging risks (4.4.1). This was done to demonstrate the range of plant character values which could be caused by different husbandry. These treatments were generally measured frequently, but for some plant characters in the MT95 experiment infrequent measurements were made. In such cases substitute treatments were used which were identical to the high and low risk treatments except that the early PGR (5C Cycocel) and late PGR (Terpal) had been applied (high risk treatment with PGRs; low risk treatment with PGRs). After describing the seasonal development and husbandry effects on lodging-associated plant characters there is a description of the development of each plant character for five varieties. There follows a consideration of the influence of individual husbandry treatments on the growth and development of plant characters throughout their growth period. Much of the post GS 39 information for this is dependent on the MT96 experiment, which was sampled less frequently, but for more treatments than the MT95 experiment.

5.1 THE STEM BASE COMPONENT OF THE MODEL

Stem base failure moment is calculated from the external stem diameter, stem wall thickness and failure yield stress. The seasonal development and the influence of husbandry will be considered for stem base failure moment and its component parts.

5.1.1 Growth and development for the high and low risk treatments

Stem base failure moment and stem diameter were considerably greater in the MT95 experiment than the MT96 experiment. During grain filling the MT95 high risk treatment had a stem base failure moment of 0.14 Nm compared with just 0.06 Nm in the MT96 experiment. This clearly demonstrates the importance of the crop in causing seasonal variation in lodging risk.

In the MT95 and MT96 experiments stem base failure moment showed its maximum value during anthesis, before steadily decreasing to just over half of its maximum value close to harvest (Figure 5.1 and Figure 5.2). In the MT96 experiment the decrease in stem failure moment from anthesis to harvest appeared to be due to decreases in stem diameter (Figure 5.3) and wall width (Figure 5.4). It is likely that the relatively small decreases in diameter and wall width could account for the proportionally larger decrease in failure moment when it is considered that these components are multiplied to the power of three and four respectively to calculate stem failure moment (Baker, 1995). In the MT95 experiment the decrease in stem failure moment was also accompanied by a decrease in stem diameter (Figure 5.5). Stem wall width and stem failure yield stress were not measured in this experiment. There was no consistent developmental trend for stem failure yield stress (Figure 5.6) between anthesis and harvest, which suggests that it played no part in the decrease of stem failure moment over this period. Early measurements of stem failure moment, particularly those taken at GS 33, may have been small because the material components of the stem structure were still developing. For example, at GS 33 in the MT96 experiment the small stem failure moment of the low risk treatment appeared to be strongly associated with a small failure yield stress.

In both experiments the low risk treatment had a significantly greater stem failure moment than the high risk treatment due to a greater stem diameter and stem wall width. These large differences were present between GS 39 and harvest. In the MT96 experiment the stem base of the low risk treatment was almost three times stronger than for the high risk treatment. Thus husbandry strategy is very important in determining stem strength.

Stem failure yield stress showed no consistent differences between the high and low risk treatments and therefore did not appear to be a cause of the differences in stem failure moment. However, stem failure yield stress was quite variable, with large SEDs (Table 5.4), in comparison with the much smaller variation for stem diameter and wall width. More precise measurements of this plant character will be required to confirm its lack of plasticity due to husbandry.

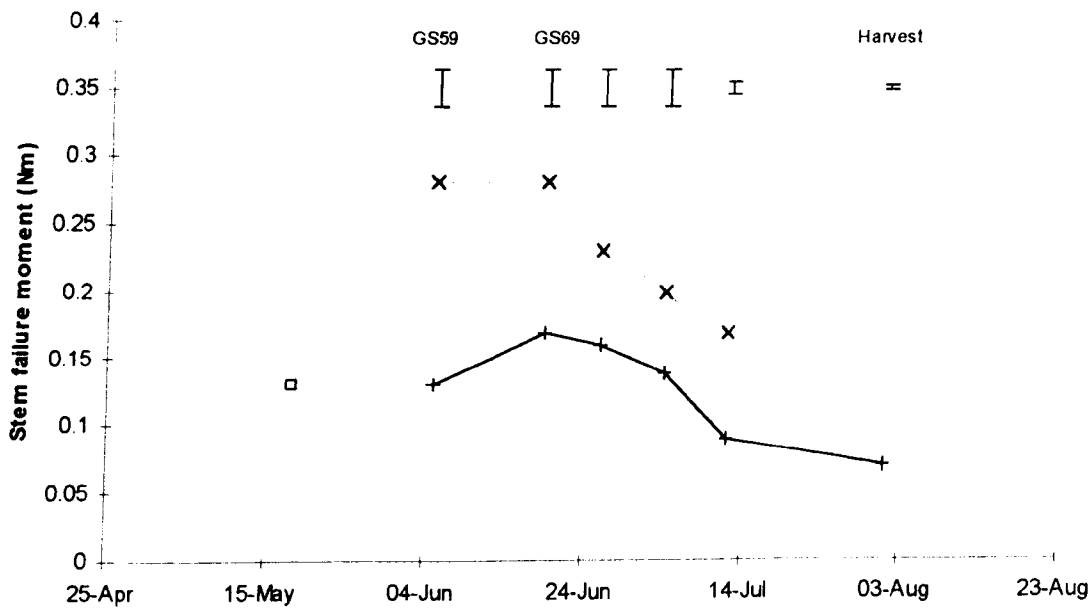

Figure 5.1 The development of stem failure moment in the MT95 experiment season for the high (— + —) and low (- -x- -) risk treatments, both with early and late PGRs. Bars represent ± SEM (2 df).

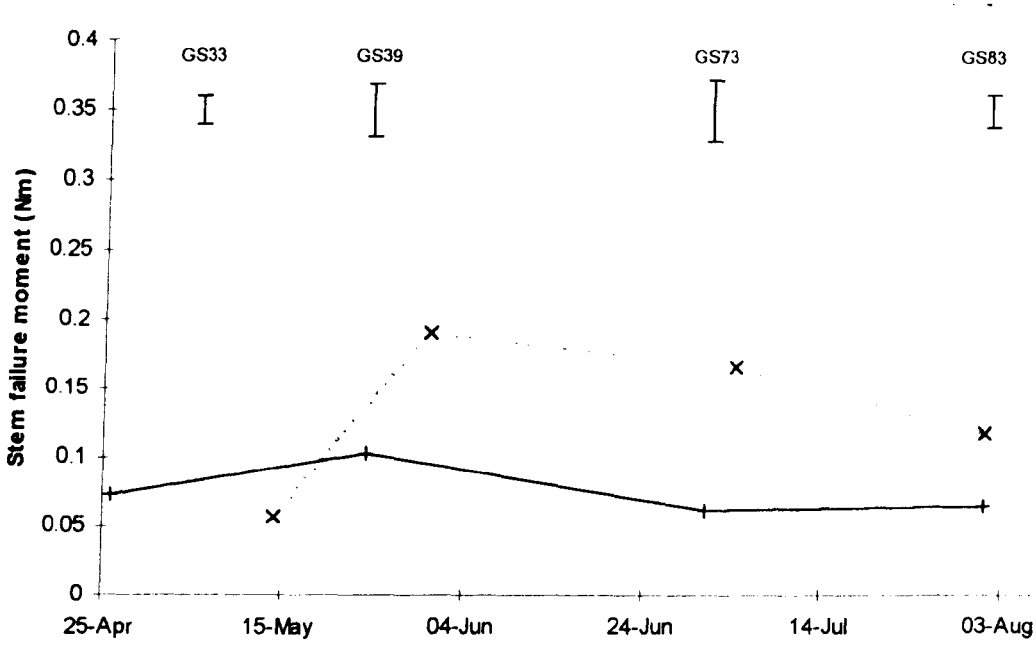

Figure 5.2 The development of stem failure moment in the MT96 experiment growing season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (23-40 df, see Appendix 5).

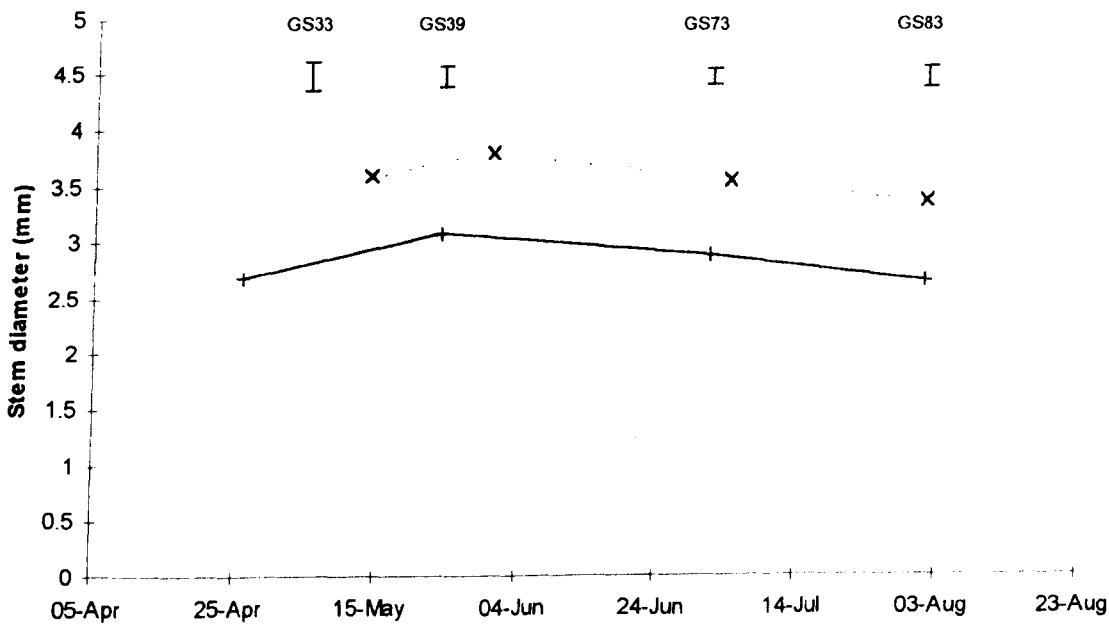

Figure 5.3 The development of stem diameter in the MT96 experiment growing season for the high (— + —) and low (- -×- -) risk treatments Bars represent ± SEM (23-40 df, see Appendix 5).

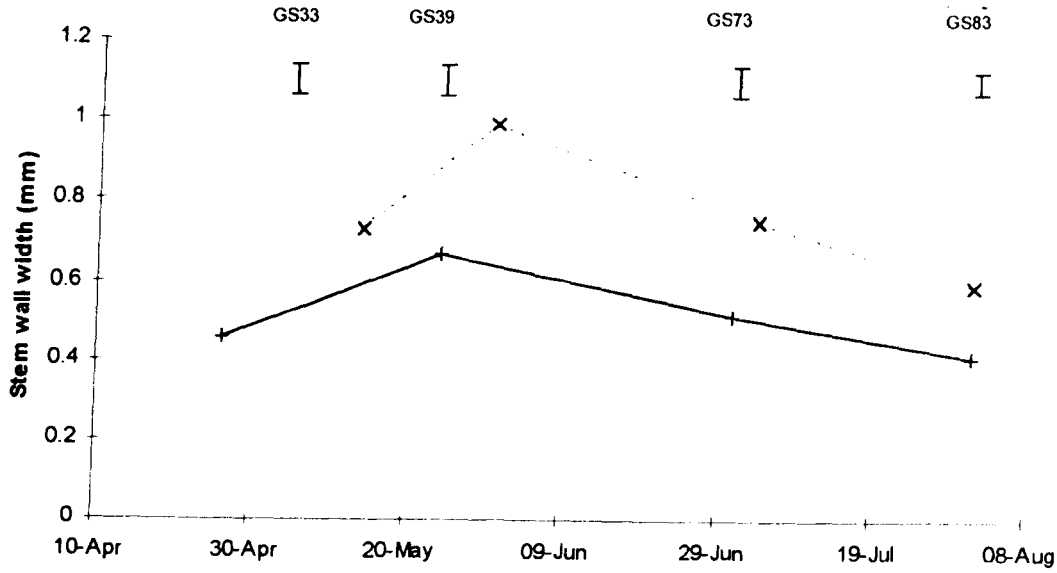

Figure 5.4 The development of stem wall width in the MT96 experiment growing season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (23-40 df, see Appendix 5).

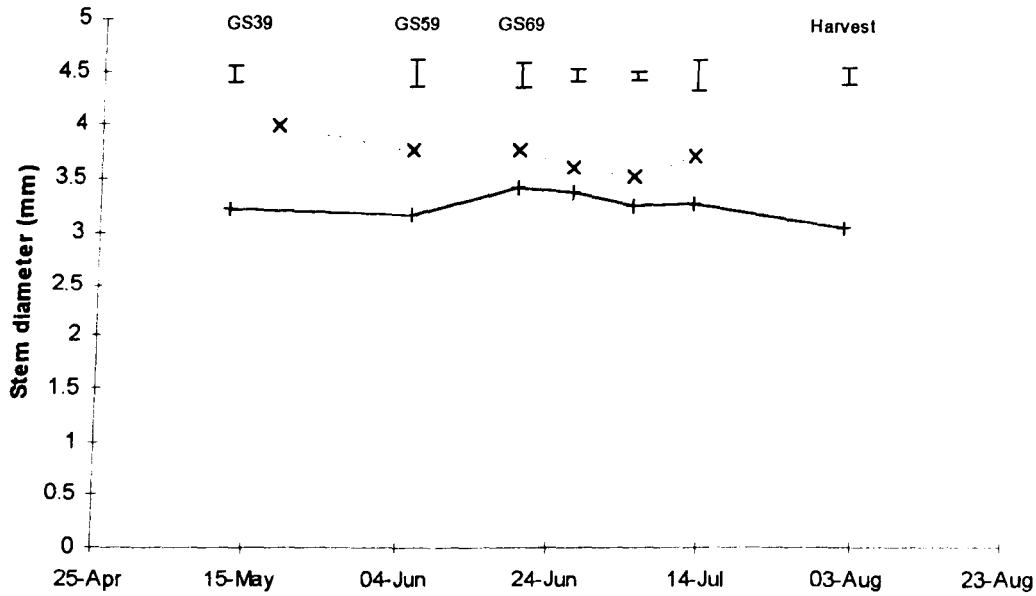

Figure 5.5 The development of stem diameter in the MT95 experiment growing season for the high (— + —) and low (- -×- -) risk treatments, both with early and late PGRs. Bars represent ± SEM (2 df).

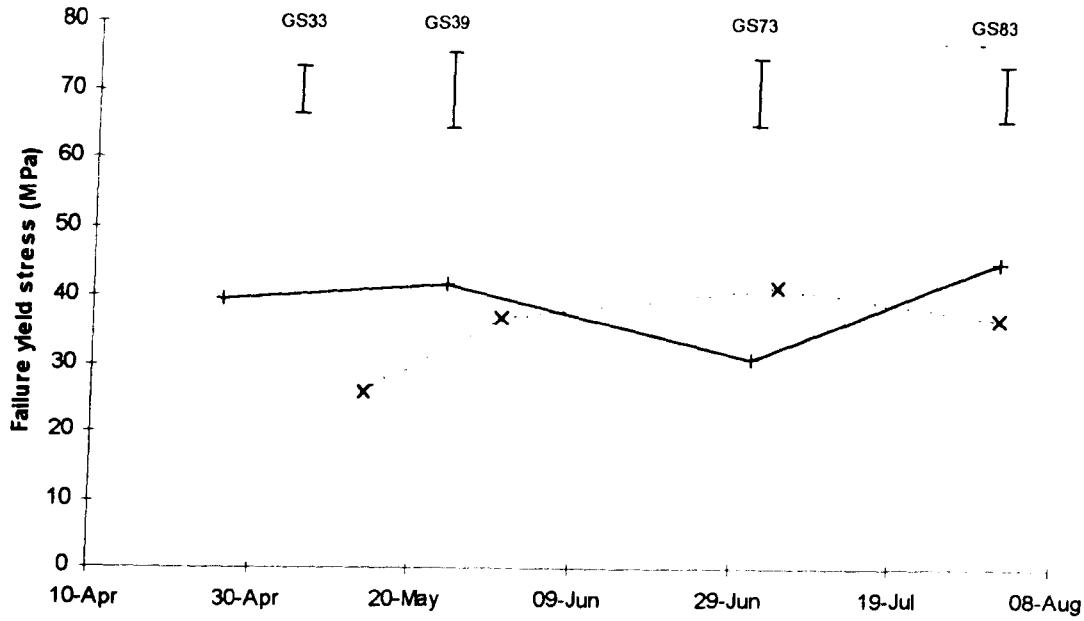

Figure 5.6 The development of failure yield stress in the MT96 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-40 df, see Appendix 5).

5.1.2 The influence of variety

Measurements of stem failure moment and its components in the VT95 experiment were taken for the core subset of varieties at GS 39 and GS 61 + 75 °Cd. These measurements give information about genotypic variation of stem failure moment and its components and whether the early development of these plant characters changes with genotype.

Statistically significant differences were found between the varieties for stem failure moment (Figure 5.7), stem failure yield stress (Figure 5.8), stem diameter (Figure 5.9) and stem wall width (Figure 5.10) at GS 39 and GS 61 + 75 °Cd ($P<0.05$). The varietal range in stem failure moment at GS 61 + 75 °Cd was moderate, 0.17 Nm for Little Joss compared with 0.23 Nm for Riband. This was an expected difference since modern varieties are perceived to have 'stronger' straw, although more varieties must be tested to prove this. A large varietal range was observed for the components of stem failure moment, however no one component appeared to influence stem failure moment more than the others.

Between GS 39 and anthesis, stem failure moment of all varieties decreased due to a diminishing stem diameter and wall width, as did Mercia in the MT95 and MT96 experiments. However, the rate of decrease in stem failure moment depended on genotype. Failure yield stress did not change significantly between GS 39 and anthesis and varietal differences were consistent between GS 39 and GS 61 + 75 °Cd (Figure 5.8).

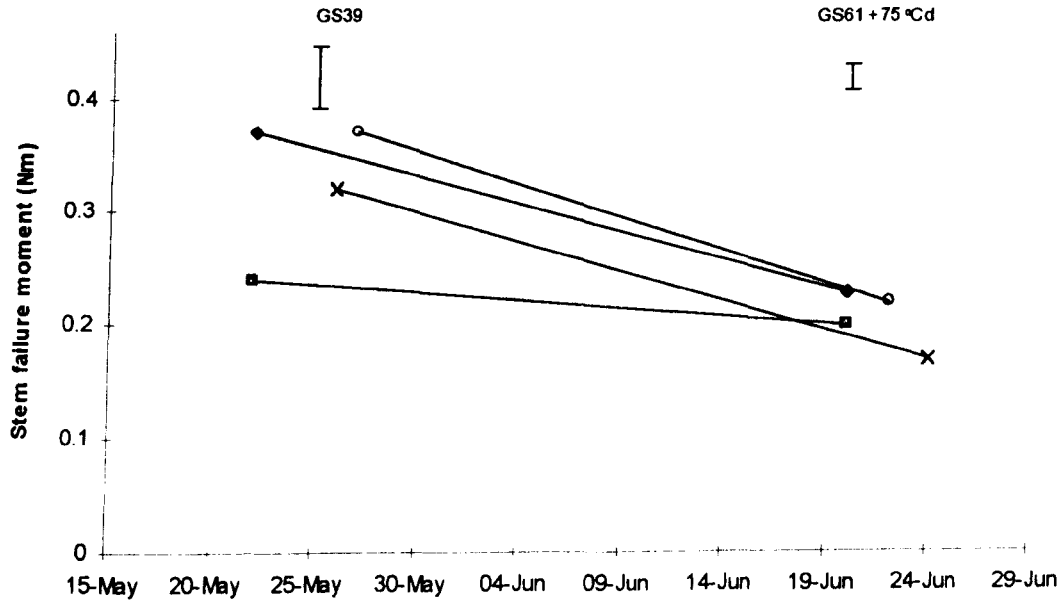

Figure 5.7 The development of stem failure moment in the VT95 experiment for varieties Riband (◆), Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (6 df).

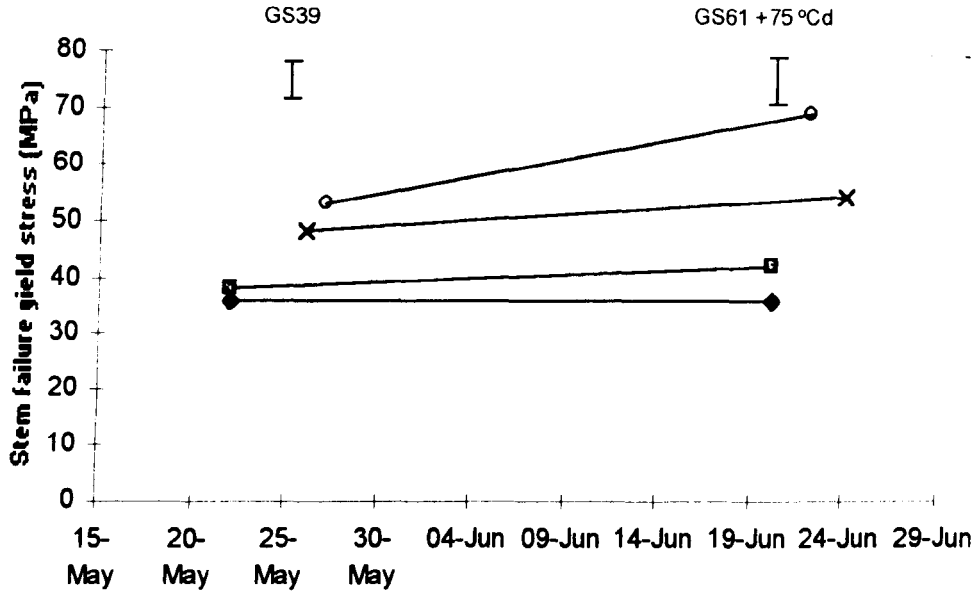

Figure 5.8 The development of stem failure yield stress in the VT95 experiment for varieties Riband (◆), Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (6 df).

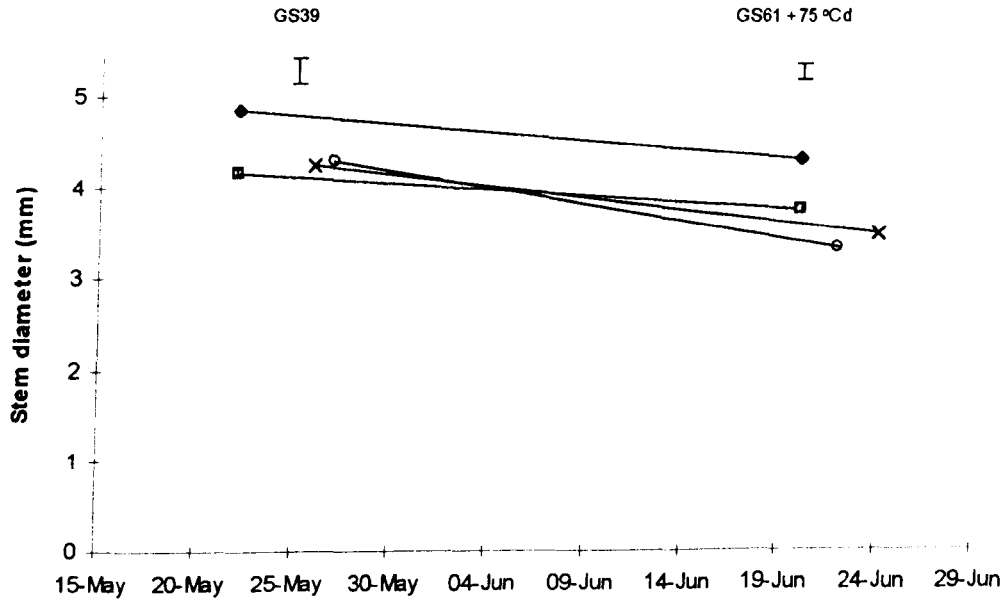

Figure 5.9 The development of stem diameter in the VT95 experiment for varieties Riband (◆), Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (6 df).

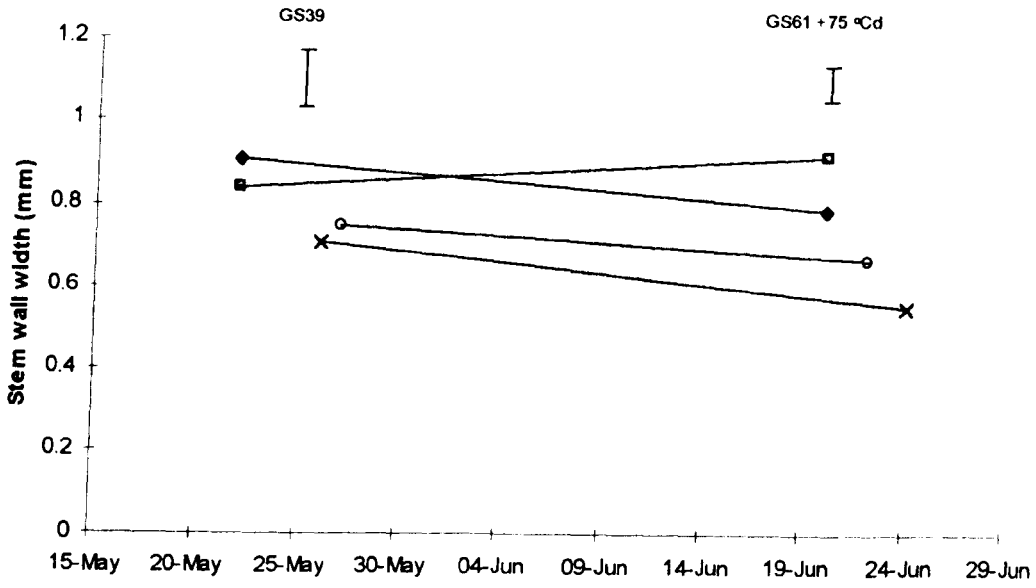

Figure 5.10 The development of stem wall width in the VT95 experiment for varieties Riband (◆), Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (6 df).

5.1.3 The influence of husbandry on the stem base

The best description of how husbandry affects the stem base components comes from the MT96 experiment. In the MT95 experiment only stem diameter was measured for each individual husbandry treatment. The other stem base components were measured for the high and low risk treatments with PGRs.

Sowing date

In the MT96 experiment, early sowing decreased stem failure moment at GS 39 and GS 71 (Table 5.1) due to decreases in stem diameter (Table 5.2) and stem wall width (Table 5.3). These sowing date effects were only statistically significant ($P<0.05$) at high levels of residual nitrogen and became less significant close to harvest. Nevertheless, at grain fill large differences were observed for soils with high levels of residual nitrogen, with late sown crops having an average stem failure moment of 0.16 Nm compared with only 0.10 Nm for early sown crops. In the MT95 experiment, sowing date had no statistically significant effect on the stem diameter at GS 85 (Table 5.4). However, this does not mean that stem diameter was unaffected by

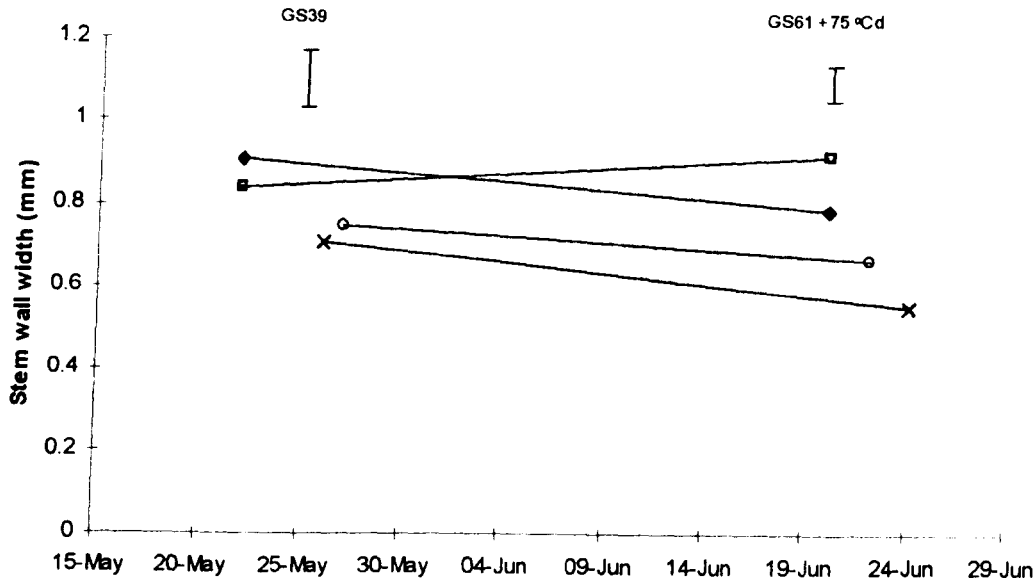

Figure 5.10 The development of stem wall width in the VT95 experiment for varieties Riband (♦), Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (6 df).

5.1.3 The influence of husbandry on the stem base

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sowing date at earlier growth stages. Stem failure yield stress (Table 5.5) was reduced by early sowing in association with high levels of soil residual nitrogen.

Seed rate

In the MT96 experiment high seed rate decreased stem failure moment due to decreases in stem diameter (Table 5.3) and wall width. These effects were statistically significant at GS 33, GS 39 and GS 83 ($P<0.05$). At GS 71 (Table 5.2) the effect on stem failure moment was not quite statistically significant ($P=0.1$). Overall, the effect of seed rate on stem strength was smaller than that of sowing date at high levels residual nitrogen. In the MT95 experiment high seed rate decreased stem diameter at GS 39 ($P<0.05$), but differences became less significant towards harvest. At GS 85 this effect was only statistically significant for the early sown treatment (Table 5.4). As with sowing date, stem failure yield stress was unaffected by seed rate.

Residual nitrogen

In the MT96 experiment high residual nitrogen decreased stem failure moment at GS 33 and GS 73 (Table 5.1) due to decreases in stem diameter (Table 5.2), stem wall width (Table 5.3) and failure yield stress (Table 5.5). In general, these effects were only statistically significant when associated with early sowing. In the MT95 experiment the high residual nitrogen decreased stem diameter at GS 39 ($P<0.05$), but not at GS 85.

Lodging controls

Of the lodging controls Canopy Management had the most important effect on the components of stem strength. In association with high levels of residual nitrogen, Canopy Management caused greater stem diameters and wall widths compared with the nil lodging control ($P<0.05$). For the early sown and high residual nitrogen treatment combination, this resulted in stem failure moment increasing from 0.08 Nm without Canopy Management, to 0.12 Nm with Canopy Management (Table 5.1). This represents an important method by which potentially weak stems can be strengthened. The PGR lodging control treatments generally had no statistically

significant effect on stem failure moment or its components. In the MT96 experiment 5C Cycocel caused a significantly smaller failure yield stress at GS 33 and GS 71 compared with the nil lodging control treatment ($P<0.05$) (Table 5.5). However, the resulting effect on stem failure moment was small.

Table 5.1 Stem failure moment (Nm) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	0.063	0.100	0.149	0.159
residual	5C Cycocel (PGR)	0.072	0.115	0.134	0.148
nitrogen	Canopy Management	0.116	0.120	0.167	0.180
Low soil	Nil spring lodging control	0.160	0.188	0.152	0.166
residual	5C Cycocel (PGR)	0.123	0.150	0.124	0.166
nitrogen	Canopy Management	0.125	0.176	0.161	0.151

SED = 0.0322 (40 df)

Table 5.2 Stem diameter (mm) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	2.92	3.21	3.29	3.49
residual	5C Cycocel (PGR)	2.87	3.24	3.47	3.49
nitrogen	Canopy Management	3.29	3.25	3.41	3.58
Low soil	Nil spring lodging control	3.11	3.68	3.32	3.58
residual	5C Cycocel (PGR)	3.27	3.50	3.39	3.59
nitrogen	Canopy Management	3.05	3.37	3.33	3.42

SED = 0.138 (40 df)

Table 5.3 Stem wall width (mm) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	0.517	0.553	0.613	0.645
residual	5C Cycocel (PGR)	0.531	0.601	0.625	0.672
nitrogen	Canopy Management	0.610	0.636	0.710	0.723
Low soil	Nil spring lodging control	0.618	0.692	0.639	0.750
residual	5C Cycocel (PGR)	0.642	0.660	0.663	0.694
nitrogen	Canopy Management	0.595	0.656	0.675	0.680

SED = 0.0563 (40 df)

Table 5.4 Stem diameter (mm) at GS 85 for the MT95 experiment

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	2.96	3.36	3.22	3.34
residual	5C Cycocel (PGR)	3.08	3.40	3.12	3.46
nitrogen	5C Cycocel + Terpal (PGR)	3.10	3.36	3.26	3.54
Low soil	Nil spring lodging control	3.04	3.36	3.30	3.32
residual	5C Cycocel (PGR)	3.28	3.36	3.28	3.44
nitrogen	5C Cycocel + Terpal (PGR)	3.14	3.30	3.02	3.40

SED = 0.134 (40 df)

Table 5.5 Stem failure yield stress (Mpa) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	31.0	37.3	48.6	45.5
residual	5C Cycocel (PGR)	35.9	39.7	38.5	42.0
nitrogen	Canopy Management	38.1	40.5	47.8	45.9
Low soil	Nil spring lodging control	62.7	44.5	49.8	41.6
residual	5C Cycocel (PGR)	41.2	39.7	37.4	42.4
nitrogen	Canopy Management	50.5	54.7	51.3	44.2

SED = 6.86 (40 df)

5.1.4 Summary

The large decrease in stem failure moment between GS 39 and harvest appeared to be due to stems becoming narrower and thinner walled. These effects may have occurred as the stem dried out and became less turgid. This trend for a progressively weaker stem would be expected to increase the risk of stem lodging between GS 39 and harvest. There was no evidence for weakening of the stem due to relocation of structural stem carbohydrates to the growing grains because the strength of the stem material (failure yield stress) did not change.

The effect of season and most husbandry treatments on stem failure moment were through changing stem diameter and wall width. The high shoot numbers and large canopy sizes observed during early stem extension in the high risk husbandry treatments and in the MT96 experiment as a whole may have caused the stems to etiolate, resulting in weaker, narrower stems with thinner walls. Variation in stem failure moment due to husbandry was larger than the genotypic variation, for the varieties tested. Genotypic variation was due to variation in all components of stem failure moment including failure yield stress.

Canopy Management was the most effective remedial control for preventing potentially weak stems. Smaller early nitrogen applications limit tillering and canopy

expansion at the beginning of stem extension. On balance this may increase the assimilate supply per stem and reduce stem etiolation, resulting in stronger, wider stems with thicker walls.

Crucially, stem failure moment and its components cannot be measured before GS 33 or GS 39. This means that a prediction of stem failure moment at GS 30 would have to rely on other indicative measurements. For prediction schemes made after GS 33 a method of accounting for the decline of stem failure moment due to diminishing stem diameter and wall width must be found. In addition, this would have to suit individual varieties, which varied in the rate of decline of stem failure moment. Failure yield stress appeared to remain unchanged thoughout stem development, despite its high variability, and therefore might prove simpler to predict.

5.2 AERIAL COMPONENTS OF THE MODEL FOR A SINGLE SHOOT

The aerial components required by the model to calculate the base bending moment of a single shoot include natural frequency and height at centre of gravity. Natural frequency is affected by a number of components, the most important of which is height at centre of gravity; greater heights result in smaller natural frequencies (Baker, 1995). Less important components include stem stiffness and root ball resistance (which are both positively related with natural frequency) and ear weight (which is negatively related with natural frequency). Characters which influence height at centre of gravity, include plant height, stem and leaf fresh weight and ear fresh weight.

5.2.1 The growth and development for the high and low risk treatments

Natural frequency

Natural frequency became progressively smaller from GS 39 onwards (causing base bending moment to increase) and reached its lowest values during the grain filling period in July. Natural frequency then increased sharply in the two weeks prior to harvest (Figure 5.11 and Figure 5.12). Between GS 39 and harvest the high risk treatment generally had a significantly smaller natural frequency than the low risk

treatment ($P<0.05$). During grain filling in the MT95 experiment the low risk treatment had a natural frequency of 1.24 Hz compared with only 0.85 Hz for the high risk treatment. The high risk treatment plants therefore had a greater base bending moment and increased lodging risk.

Height at centre of gravity and its components

In the MT95 and MT96 experiments height at centre of gravity increased by up to 25 cm between GS 39 and harvest (Figure 5.13 and Figure 5.14). These increases doubled the height at centre of gravity in some instances and considerably increased the crop's base bending moment and lodging risk nearer harvest. Increases in the height at centre of gravity were due to an increase in the height to the top ligule (or ear collar), a decrease in leaf and stem fresh weight per shoot and an increase in ear fresh weight. Height to the top ligule increased until June (anthesis) (Figure 5.15 and 5.16) and probably accounted for the increase in height at centre of gravity from GS 39 to anthesis. Ear fresh weight increased from less than 2 g at ear emergence to about 4 g during grain filling, before declining to less then 2 g at harvest (Figure 5.17; it should be noted that the harvest time value of ear fresh weight is for the grain fresh weight only). The change in ear weight may account for the increase in height at centre of gravity after the stem had finished extending. Combined leaf and stem fresh weight per shoot decreased dramatically from about 9 g at GS 39 to less then 2 g at harvest (Figure 5.18) and may have influenced the final increase in height at centre of gravity before harvest. It should be admitted that leaf and stem fresh weight may not always relate negatively to height at centre of gravity because the relationship also depends on the weight distribution of the stem and leaves.

Between GS 39 and harvest, in both experiments, the high risk treatment had a significantly greater height at centre of gravity than the low risk treatment ($P<0.05$; Figure 5.13 and Figure 5.14). This difference amounted to 2 cm and 5 cm in the MT95 and MT96 experiments respectively. These relatively small differences were probably due to the statistically significant differences in plant height ($P<0.05$; Figure 5.15 and 5.16).

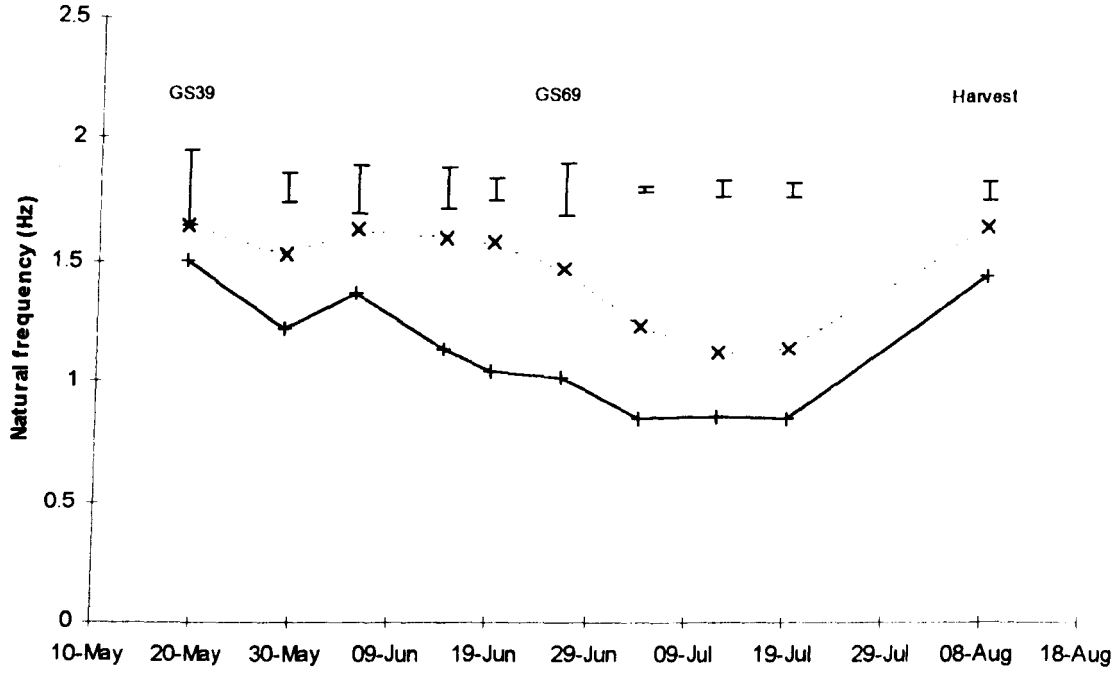

Figure 5.11 The development of natural frequency in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments with PGRs. Bars represent ± SEM (2 df).

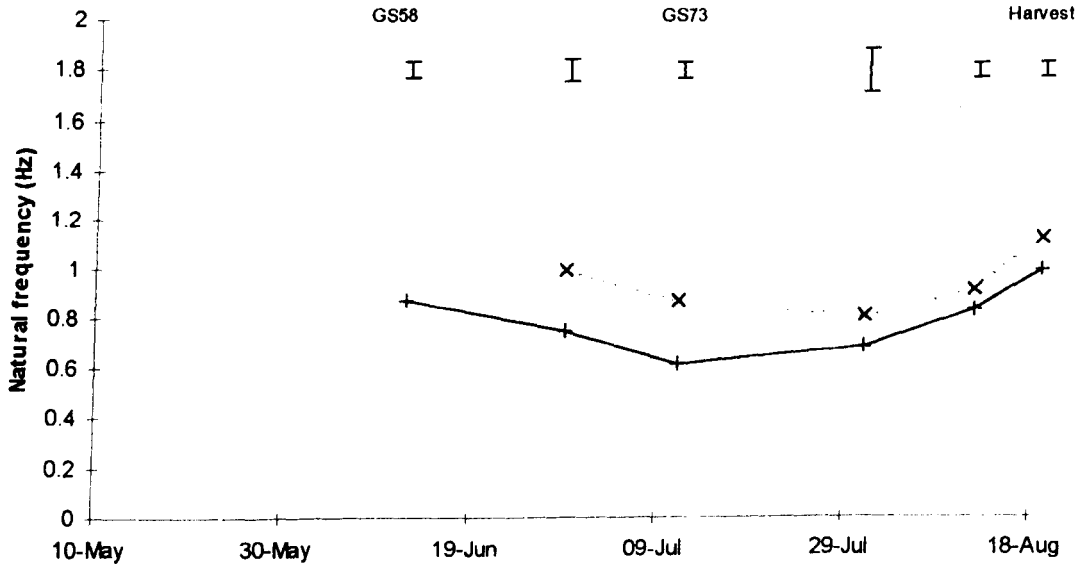

Figure 5.12 The development of natural frequency in the MT96 experiment growing season for the early sown (— + —) and late sown (- -x- -) treatments. Bars represent ± SEM (2-56 df, see Appendix 5).

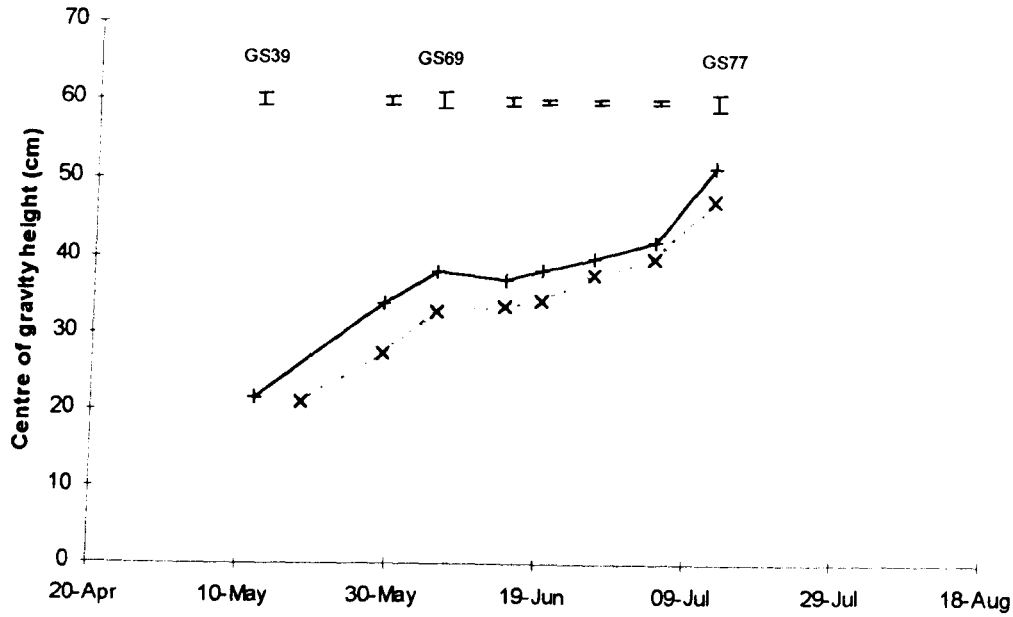

Figure 5.13 The development of height at centre of gravity in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments with PGRs. Bars represent ± SEM (2 df).

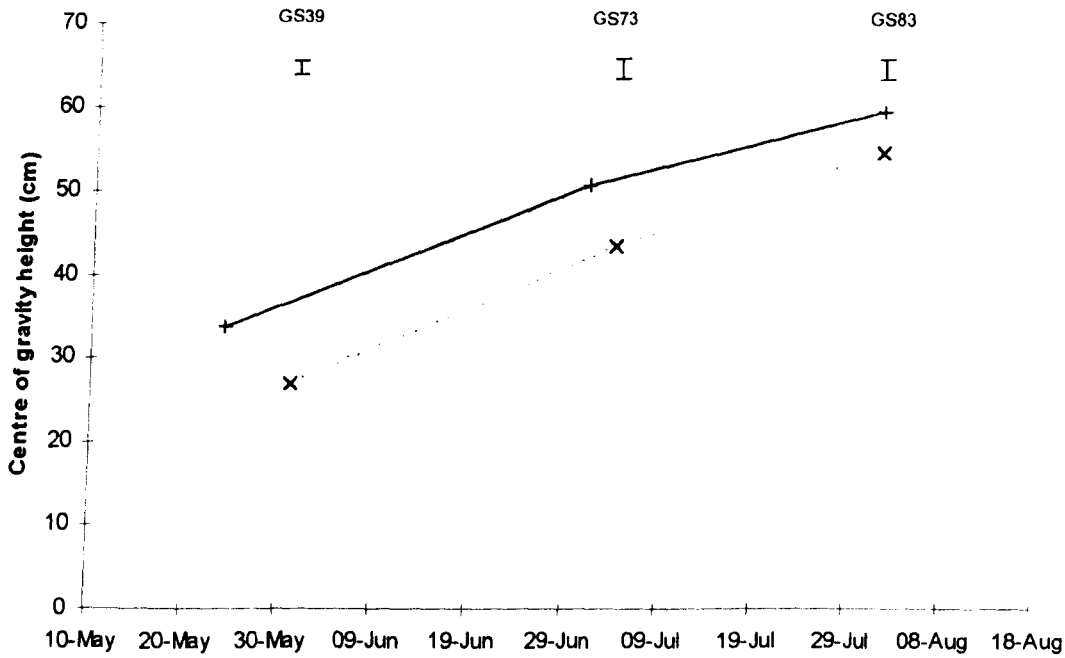

Figure 5.14 The development of height at centre of gravity in the MT96 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

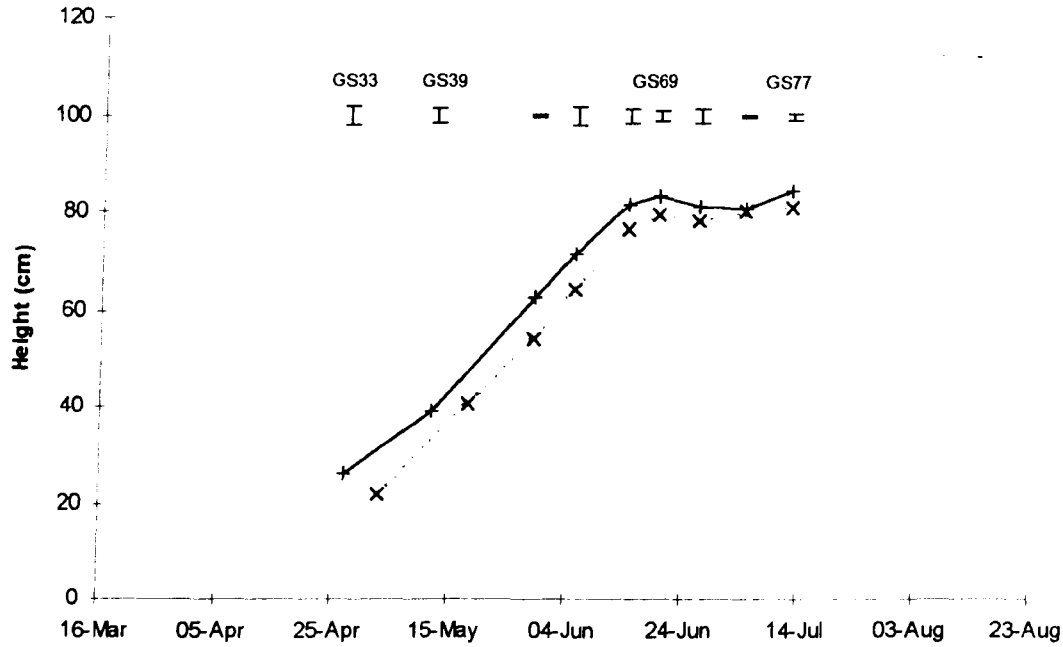

Figure 5.15 The development of height to top ligule or to ear tip in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments with PGRs. Bars represent ± SEM (2-56 df, see Appendix 5).

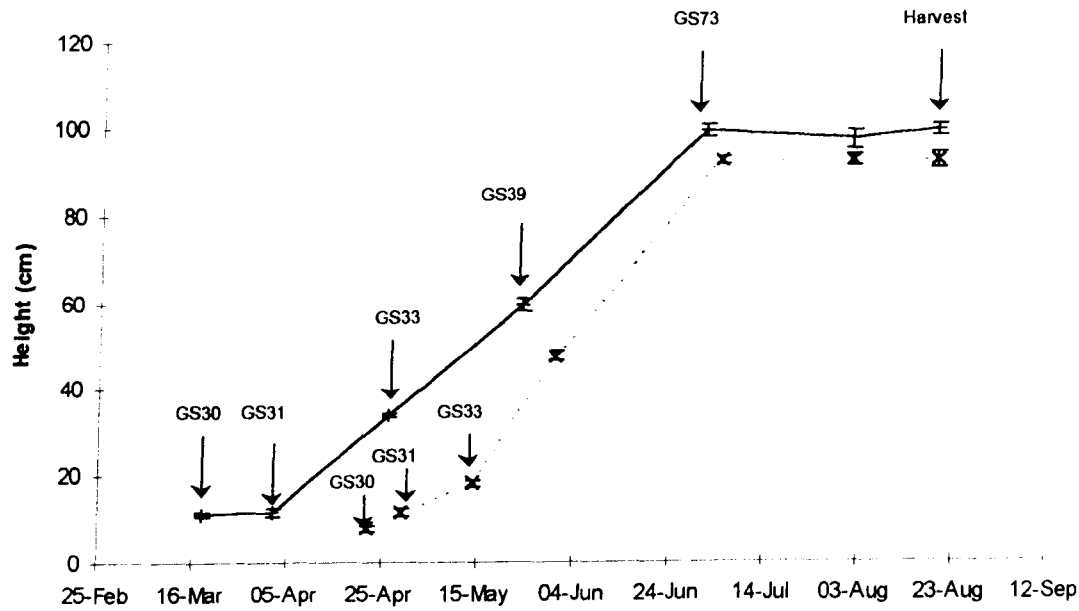

Figure 5.16 The development of height to top ligule or ear tip in the MT96 growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

Nb When growth stage dates are very different the error bar is appended to each data point.

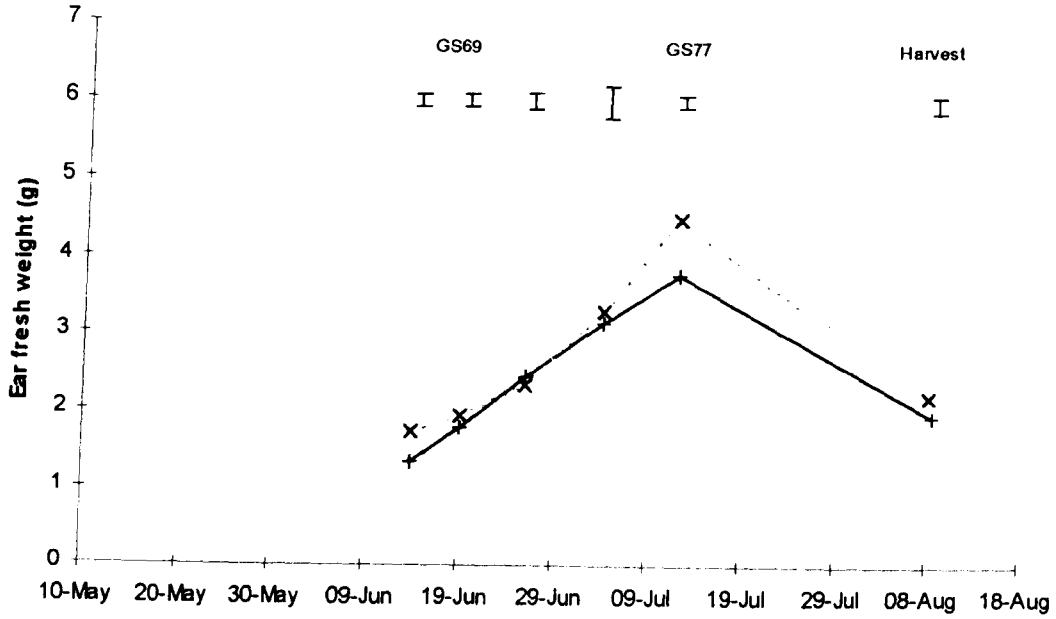

Figure 5.17 The development of ear fresh weight in the MT95 growing season for the high (— + —) and low (- -x- -) risk treatments with PGRs. Bars represent ± SEM (2 df).

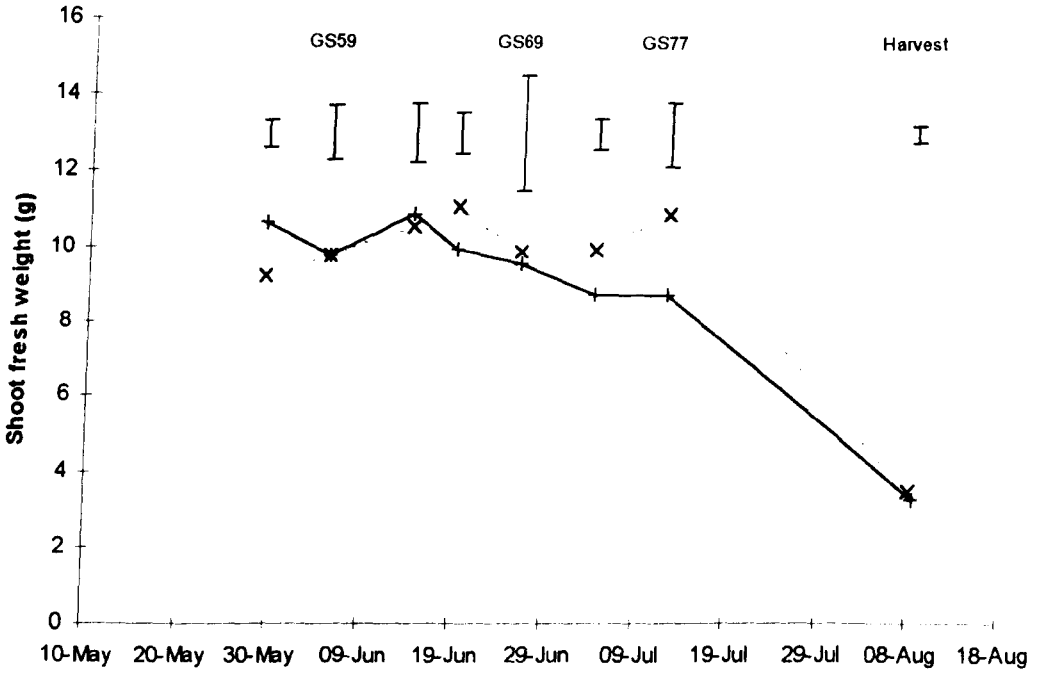

Figure 5.18 The development of combined stem and leaf fresh weight in the MT95 growing season for the high (— + —) and low (- -x- -) risk treatments with PGRs. Bars represent ± SEM (2 df).

5.2.2 The influence of variety

Natural frequency was measured at GS 75 in the VT95 experiment. Highly significant differences were found between 16 varieties ($P<0.01$) (Griffin, 1998). A wide range of values was observed, from 0.56 Hz for Little Joss to 0.96 Hz for Hereward. Smaller but still highly significant variation was observed amongst the modern cultivars, from 0.74 Hz for Spark to 0.96 Hz for Hereward. Height at centre of gravity was measured for five varieties at GS 39 and GS 61 + 75 °Cd (Figure 5.19). A larger subset of varieties was measured at GS 61 + 75 °Cd (see Appendix 2.3). Significant differences were found between the varieties ($P<0.05$), whose rankings were consistent between GS 39 and GS 61 + 75 °Cd. Amongst the modern varieties large variation in height at centre of gravity was observed at GS 61 + 75 °Cd, with 36 cm for Rialto and 44 cm for Spark.

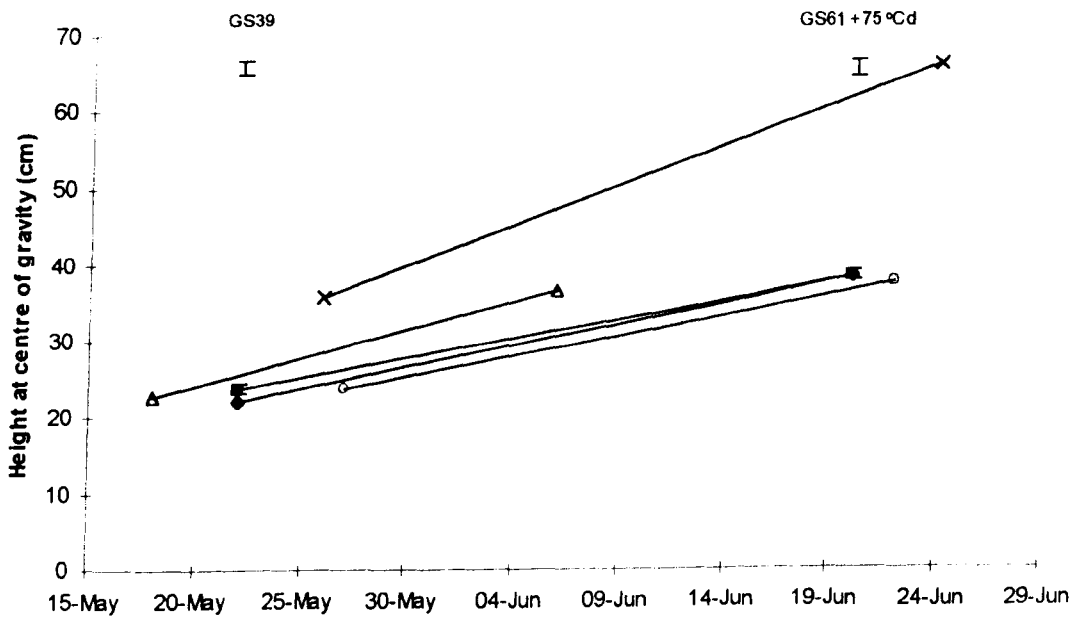

Figure 5.19 The development of height at centre of gravity in the VT95 experiment for varieties Riband (◆), Mercia (Δ),Hereward (■), Little Joss (×) and Beaver (o). Bars represent ± SEM (8 df).

5.2.3 The influence of individual husbandry treatments

Natural frequency was measured for all husbandry treatments at GS 85 in the MT95 experiment (Table 5.6) and at GS 73 in the MT96 experiment (Table 5.7). Height at centre of gravity was measured for all husbandry treatments at GS 71 in the MT95 experiment (Table 5.8) and at GS 73 in the MT96 experiment (Table 5.9). In the MT96 experiment natural frequency and height at centre of gravity were also measured at GS 85, but for a smaller number of treatments. Plant height was measured frequently in both lodging experiments for all treatments. Plant heights for the MT95 experiment at GS 71 and for the MT96 experiment at GS 73 are shown in Table 5.10 and Table 5.11. Combined leaf and stem fresh weight was only measured for the high and low risk treatments with PGRs and has already been described. Grain fresh weight per ear was measured for all treatments at harvest in both lodging experiments (Table 5.12 and Table 5.13), and is used here as a substitute for ear fresh weight.

Sowing date

In the MT96 experiment, early sowing decreased natural frequency at GS 73 (Table 5.7) and GS 85 ($P<0.05$), and increased height at centre of gravity at GS 39, GS 73 (Table 5.9) and GS 85 ($P<0.05$). On average, early sowing decreased natural frequency from 0.91 to 0.74 Hz and increased height at centre of gravity from 0.42 to 0.46 m compared with late sowing at GS 73. A plant height increase of eight centimetres due to early sowing probably caused these differences (Table 5.11; $P<0.05$), despite early sown crops showing a small but significant reduction in grain fresh weight (Table 5.13; $P<0.05$). In the MT95 experiment fewer days separated the sowing dates and no difference was found in plant height (Table 5.10). This probably explains why there were no sowing date effects on either natural frequency (Table 5.6), or height at centre of gravity (Table 5.8).

Seed rate

The main effect of seed rate was for high seed rate to decrease natural frequency in both experiments. In the MT96 experiment seed rate had a smaller effect than sowing

date, with high seed rate causing an average natural frequency of 0.79 Hz compared with 0.86 Hz for the low seed rate. Importantly, seed rate had no effect on height at centre of gravity or plant height in either experiment. This means that seed rate affected natural frequency without changing its main component, height at centre of gravity. Therefore one of the other, less important, components of natural frequency must have been influencing it. High seed rate had a significantly lower grain fresh weight per ear at harvest than the low seed rate in both experiments ($P<0.05$). However, this would be expected to increase natural frequency rather than cause a decrease as was observed. This suggests that high seed rate reduces natural frequency either by reducing stem stiffness or root ball resistance.

Residual nitrogen

In the early sowings of the MT96 experiment, high residual nitrogen decreased natural frequency from 0.77 to 0.71 Hz ($P<0.05$) and increased height at centre of gravity from 44 cm to 45 cm ($P=0.09$) compared with low residual nitrogen. High residual nitrogen decreased grain fresh weight per ear at harvest in both the MT95 ($P<0.05$) and MT96 ($P<0.01$) experiments. As with the seed rate effect, residual nitrogen appears to have affected natural frequency without having a large effect on height at centre of gravity. Once again, it seems that high residual nitrogen reduced natural frequency either by decreasing stem stiffness or root ball resistance. In the MT95 experiment, in which the differences in soil residual nitrogen were smaller, no effect on natural frequency was found.

Lodging controls

The lodging control treatments significantly reduced natural frequency ($P<0.01$) and height at centre of gravity ($P<0.001$) in both experiments due to a decrease in plant height. In the MT96 experiment the average natural frequency and height at centre of gravity was 0.72 Hz and 0.48 m for nil lodging control, 0.79 Hz and 0.45 m for Canopy Management, 0.87 Hz and 0.43 m for 5C Cycocel and 0.93 Hz and 0.41 m for 5C Cycocel with Terpal. Canopy Management also had a significantly greater grain fresh weight per ear at harvest than the other lodging control treatments in the

MT95 experiment ($P<0.001$), which would have increased height at centre of gravity and reduced natural frequency. This effect was not found in the MT96 experiment.

Table 5.6 Natural frequency (Hz) at GS 85-87 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	0.86	0.91	0.84	0.86
soil	5C Cycocel (PGR)	1.08	1.09	1.06	0.84
residual	5C Cycocel + Terpal (PGR)	1.02	1.22	1.20	1.06
nitrogen	Canopy Management	0.86	0.85	0.81	1.22
Low	Nil spring lodging control	0.84	0.86	0.88	0.85
soil	5C Cycocel (PGR)	1.04	1.04	1.09	1.10
residual	5C Cycocel + Terpal (PGR)	1.34	1.24	1.19	1.22
nitrogen	Canopy Management	0.89	0.89	0.86	0.84

SED = 0.054 (56 df)

Table 5.7 Natural frequency (Hz) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	0.56	0.62	0.75	0.87
soil	5C Cycocel (PGR)	0.73	0.74	0.95	0.98
residual	5C Cycocel + Terpal (PGR)	0.80	0.86	0.95	1.05
nitrogen	Canopy Management	0.61	0.79	0.88	0.90
Low	Nil spring lodging control	0.63	0.68	0.81	0.83
soil	5C Cycocel (PGR)	0.81	0.82	0.92	1.01
residual	5C Cycocel + Terpal (PGR)	0.88	0.89	0.94	1.09
nitrogen	Canopy Management	0.67	0.79	0.82	0.88

SED = 0.058 (56 df)

Table 5.8 Height at centre of gravity (cm) at GS 69-71 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	46.7	44.4	44.8	46.8
soil	5C Cycocel (PGR)	43.9	40.1	40.0	40.9
residual	5C Cycocel + Terpal (PGR)	40.0	38.2	36.0	36.4
nitrogen	Canopy Management	42.3	40.1	42.5	41.9
Low	Nil spring lodging control	45.3	44.6	42.4	44.7
soil	5C Cycocel (PGR)	39.1	41.3	38.8	38.2
residual	5C Cycocel + Terpal (PGR)	36.7	37.4	36.4	37.9
nitrogen	Canopy Management	39.9	39.1	41.6	40.8

SED = 1.72 (56 df)

Table 5.9 Height at centre of gravity (cm) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	51.3	51.9	45.0	46.0
soil	5C Cycocel (PGR)	45.7	45.9	41.1	41.7
residual	5C Cycocel + Terpal (PGR)	42.4	45.6	38.6	38.7
nitrogen	Canopy Management	46.2	46.4	44.3	42.8
Low	Nil spring lodging control	52.1	47.4	43.5	44.2
soil	5C Cycocel (PGR)	45.7	47.1	38.2	40.4
residual	5C Cycocel + Terpal (PGR)	43.3	42.0	37.3	38.6
nitrogen	Canopy Management	47.4	46.3	44.7	44.5

SED = 1.32 (56 df)

Table 5.10 Plant height (cm) at GS 69-71 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	91.7	96.6	100.7	101.5
soil	5C Cycocel (PGR)	88.7	87.3	88.4	90.1
residual	5C Cycocel + Terpal (PGR)	81.4	81.4	78.0	80.5
nitrogen	Canopy Management	86.6	88.0	95.7	95.7
Low	Nil spring lodging control	95.4	95.5	96.6	98.8
soil	5C Cycocel (PGR)	85.2	87.6	86.2	87.9
residual	5C Cycocel + Terpal (PGR)	79.8	80.0	78.6	78.2
nitrogen	Canopy Management	88.6	89.1	93.2	94.5

SED = 1.70 (56 df)

Table 5.11 Plant height (cm) at GS 69-71 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	100.4	104.3	92.6	94.1
soil	5C Cycocel (PGR)	90.7	89.3	81.8	86.1
residual	5C Cycocel + Terpal (PGR)	85.9	87.6	79.3	80.7
nitrogen	Canopy Management	93.9	94.5	90.1	90.4
Low	Nil spring lodging control	97.6	95.7	87.1	92.7
soil	5C Cycocel (PGR)	88.8	92.6	81.3	83.6
residual	5C Cycocel + Terpal (PGR)	83.1	84.1	76.5	81.1
nitrogen	Canopy Management	94.9	93.5	89.7	92.9

SED = 2.83 (56 df)

Table 5.12 Grain fresh weight per ear (g) at GS 69-71 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	1.25	1.48	1.48	1.60
soil	5C Cycocel (PGR)	1.42	1.58	1.60	1.54
residual	5C Cycocel + Terpal (PGR)	1.52	1.74	1.52	1.63
nitrogen	Canopy Management	1.63	1.74	1.71	1.61
Low	Nil spring lodging control	1.56	1.58	1.55	1.60
soil	5C Cycocel (PGR)	1.57	1.57	1.62	1.65
residual	5C Cycocel + Terpal (PGR)	1.41	1.79	1.56	1.61
nitrogen	Canopy Management	1.56	1.76	1.71	1.79

SED = 0.093 (56 df)

Table 5.13 Grain fresh weight per ear at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	1.04	1.07	1.24	1.20
soil	5C Cycocel (PGR)	1.10	1.05	1.16	1.26
residual	5C Cycocel + Terpal (PGR)	0.95	1.02	1.10	1.10
nitrogen	Canopy Management	1.00	1.04	1.19	1.22
Low	Nil spring lodging control	1.04	1.19	1.21	1.30
soil	5C Cycocel (PGR)	1.06	1.09	1.25	1.28
residual	5C Cycocel + Terpal (PGR)	1.01	1.10	1.22	1.28
nitrogen	Canopy Management	1.03	1.10	1.22	1.25

SED = 0.076 (56 df)

5.2.4 Summary

The decrease of natural frequency from a peak at GS 39 to a minimum during grain filling was probably due to increasing height at centre of gravity as a result of stem extension and increasing ear weight. The sharp increase in natural frequency just before harvest may have been due to decreasing ear weight as it dried out. The patterns of development of natural frequency and height at centre of gravity show that the shoot base bending moment will increase until the end of grain filling. Thereafter height at centre of gravity continues increasing, but natural frequency also begins to increase. This will probably result in stability of the shoot base bending moment during grain ripening.

Variation in natural frequency and height at centre of gravity due to husbandry was larger than variation due to genotype. Once again this emphasises the importance of husbandry methods for reducing lodging risk. It has been shown that factors influence natural frequency and height at centre of gravity by different mechanisms. Genotype, sowing date and lodging controls exerted their influence on natural frequency and height at centre of gravity primarily by altering plant height. Seed rate and residual nitrogen appeared to exert their influence on natural frequency by affecting either stem stiffness or root ball resistance. This meant they had a very small effect on height at centre of gravity. Ear fresh weight and combined leaf and stem fresh weight were not strongly influenced by husbandry in these experiments.

5.3 AERIAL COMPONENT OF THE MODEL FOR THE WHOLE PLANT

The base bending moment of the whole plant is calculated by multiplying the shoot base bending moment by the shoot number per plant. The components required to calculate shoot base bending moment, natural frequency and height at centre of gravity have been covered in section 6.2; shoot number per plant will be considered here.

5.3.1 Growth and development of the high and low risk treatments

Fertile shoot number per plant generally decreased by about one shoot between GS 30-31 and GS 69-73 (Figure 5.20 and Figure 5.21). An exception was the low risk treatment in the MT96 experiment, in which the shoot number per plant declined rapidly by over two shoots between GS 30 and GS 33, before remaining almost constant until harvest. Unlike other treatments which tillered mainly in the autumn and reached maximum shoot number before GS 30, this treatment tillered in the spring and reached its maximum shoot number at GS 31. Shoot number per plant was always about one shoot greater in the MT96 experiment compared with the MT95 experiment. From GS 30 until harvest the high risk treatment always had significantly fewer shoots per plant than the low risk treatment ($P<0.01$). This difference was usually between one and two shoots per plant.

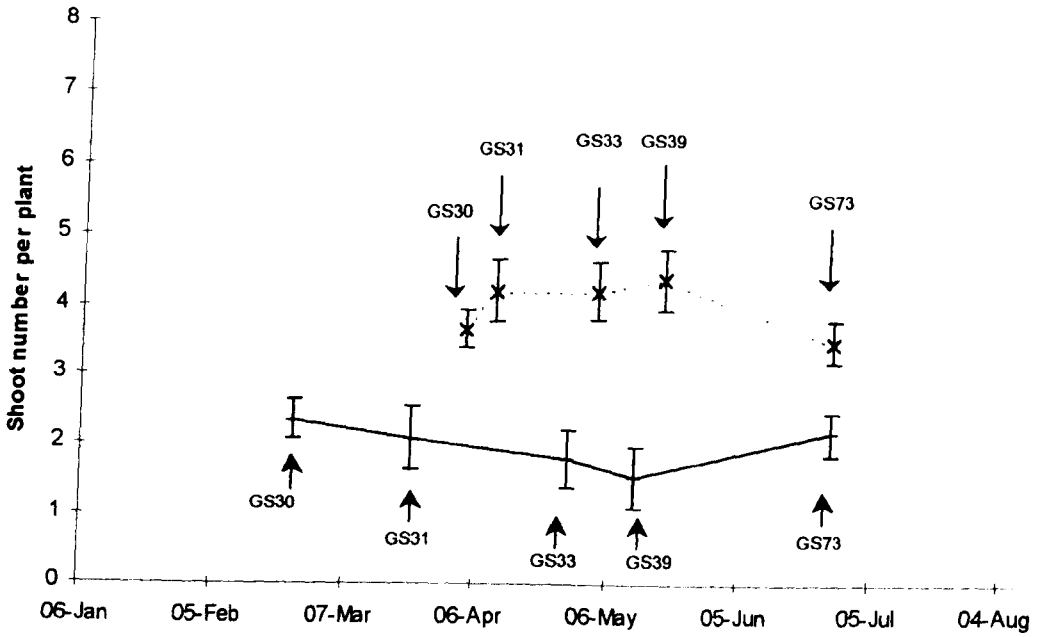

Figure 5.20 The development of shoot number per plant in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

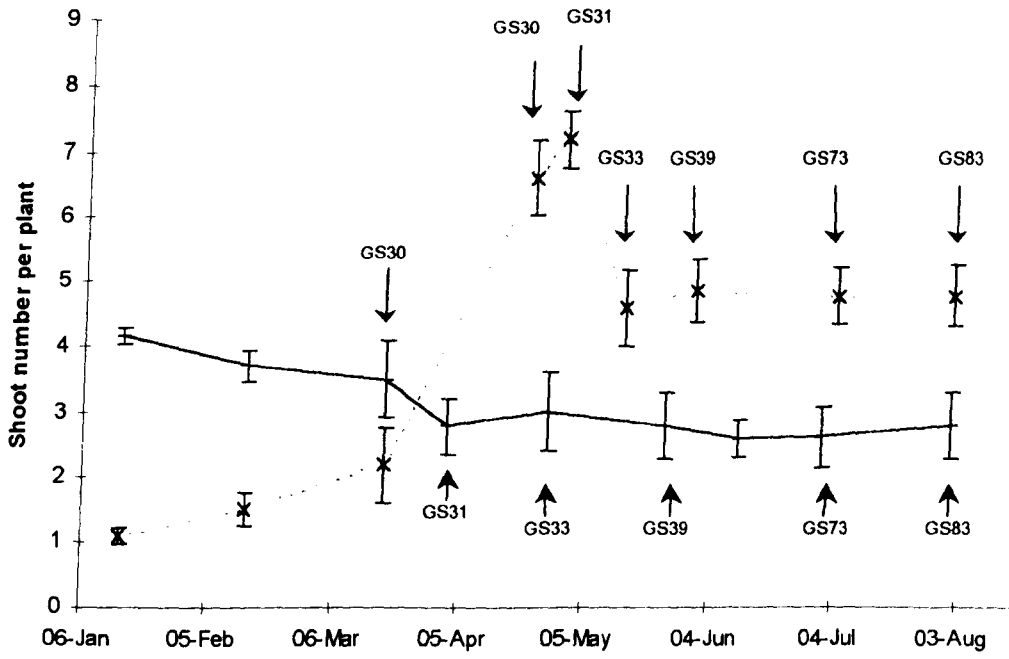

Figure 5.21 The development of shoot number per plant in the MT96 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

5.3.2 The influence of variety

Shoot number per plant was measured at GS 31, GS 39 and GS 61 + 75 °Cd for five varieties (Figure 5.22). There were statistically significant differences between these varieties at GS 31 ($P<0.05$) and GS 61 + 75 °Cd ($P<0.01$). At the later growth stage shoot number per plant varied from 1.5 for Riband to 2.8 for Spark. Varietal rankings for shoot number per plant at GS 31 changed between GS 31 and GS 61 + 75 °Cd, demonstrating that varieties differ in the proportion of their tillers which survive.

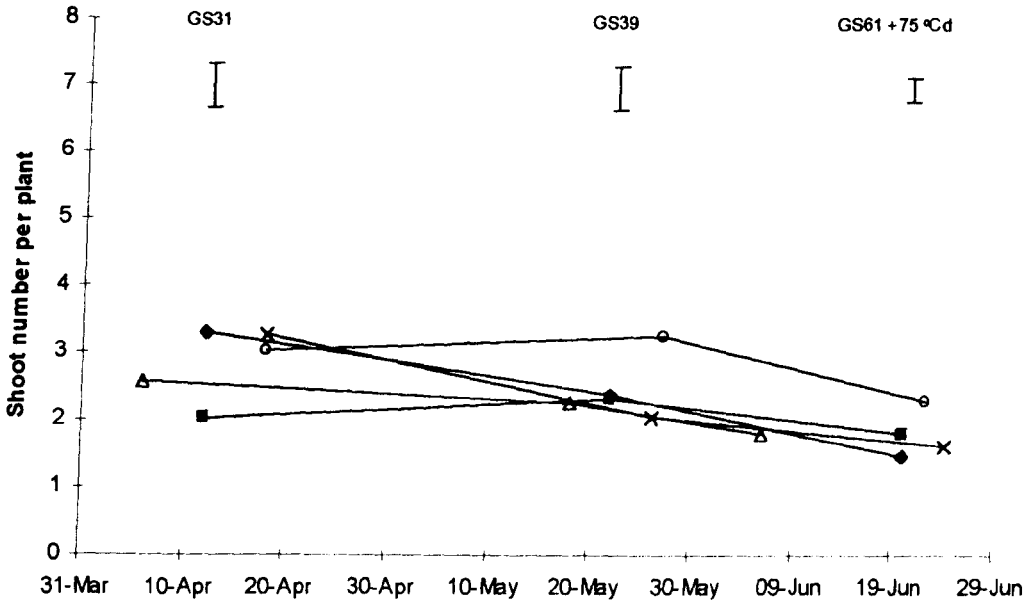

Figure 5.22 The development of shoot number per plant in the VT95 experiment for varieties Riband (◆), Mercia (Δ),Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (8 df).

5.3.3 The influence of individual husbandry treatments

Final shoot number per plant at GS 69-71 for the MT95 experiment and at GS 71-73 for the MT96 experiment are shown in Table 5.14 and Table 5.15. Low seed rate had a significantly greater shoot number per plant throughout the main growth period in both experiments ($P<0.05$), thus increasing base bending moment which the plant exerted on the anchorage system. Halving the seed rate from 500 seeds m^{-2} to 250 seeds m^{-2} caused shoot number per plant to increase from 2.0 to 3.2 in the MT95 experiment and from 3.1 to 4.5 in the MT96 experiment. In both experiments the 5C

Cycocel and the Canopy Management treatments had significantly fewer shoots per plant than the nil lodging control treatment GS 69-73 ($P<0.05$). In MT96 the nil lodging control treatment had 4.0 shoots per plant compared with 3.6 for 5C Cycocel and 3.5 for Canopy Management. In both experiments late sowing and high residual nitrogen caused small and inconsistent increases in shoot number per plant.

Table 5.14 Shoot number per plant at GS 69-71 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	2.2	3.5	2.4	3.7
soil	5C Cycocel (PGR)	2.2	2.8	2.2	3.5
residual	5C Cycocel + Terpal (PGR)	2.1	3.4	1.8	3.2
nitrogen	Canopy Management	1.7	3.2	2.1	3.4
Low	Nil spring lodging control	2.3	3.5	2.1	3.5
soil	5C Cycocel (PGR)	2.2	2.6	2.2	3.4
residual	5C Cycocel + Terpal (PGR)	2.1	3.1	1.8	3.1
nitrogen	Canopy Management	1.8	2.8	1.8	2.7

SED = 0.64 (56 df)

Table 5.15 Shoot number per plant at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	2.6	4.2	3.2	5.7
soil	5C Cycocel (PGR)	2.6	3.4	3.3	4.6
residual	5C Cycocel + Terpal (PGR)	2.9	4.8	4.2	5.2
nitrogen	Canopy Management	2.7	3.5	3.4	4.0
Low	Nil spring lodging control	2.4	5.5	3.7	4.8
soil	5C Cycocel (PGR)	2.8	4.1	3.0	4.5
residual	5C Cycocel + Terpal (PGR)	3.0	4.0	3.4	5.1
nitrogen	Canopy Management	2.3	3.4	3.1	5.2

SED = 0.44 (56 df)

5.3.4 Summary

The pattern of development for shoot number per plant was variable. For some treatments it changed very little between GS 30 and harvest, whilst decreasing significantly for other treatments. From anthesis until harvest the number of shoots per plant did not change. Large shoot number differences were observed due to season, husbandry and genotype, with seed rate causing the largest variation.

5.4 THE ANCHORAGE COMPONENT OF THE MODEL

The plant characters used by the model to calculate plant anchorage include root plate spread and the structural rooting depth. The diagram of the base of a wheat plant (Figure 2.1) shows that root plate spread is a function of rigid root length, the angle of root plate spread and the plant width at the soil surface. Structural rooting depth is a function of crown depth, rigid root length and the angle of root plate spread. All of these plant characters, except plant width at the soil surface, were measured for all treatments at growth stages GS 30, 31, 33, 39 and 69-73 in both lodging experiments. Plant width at the soil surface was measured in the MT95 experiment at GS 30, 31, 33, 39 and GS 69.

5.4.1 Growth and development for the high and low risk treatments

In the MT96 experiment, root plate spread showed a typical pattern of development (Crook *et al.*, 1994) as it increased to GS 39 then remained fairly constant until harvest (Figure 5.23). The increase in root plate spread was probably due to increasing rigid root length (Figure 5.24) and angle of root spread (Figure 5.25). Plant width at the soil surface did not appear to influence the development of root plate spread as it did not increase between GS 30 and GS 39 (Figure 5.26), although it must be noted that this was only measured in the MT95 experiment. Development of root plate spread in the MT95 experiment was not typical as it decreased from GS 30 to GS 69-71 (Figure 5.27). It is thought that very dry and strong soil conditions during the late spring and summer may have prevented complete extraction of the structural roots, resulting in a decrease in root plate spread as the season progressed.

The diminishing root plate spreads appeared to be due to decreasing rigid root length (Figure 5.28) and angle of root spread (Figure 5.29).

In both experiments the low risk treatment had a significantly greater root plate spread than the high risk treatment between GS 30 and GS 69-73 ($P<0.05$). This difference was greatest from GS 39 onwards, and at GS 85 in the MT96 experiment the high risk treatment measured 33 mm compared with 53 mm for the low risk treatment. This difference was probably due to the significantly longer rigid roots and greater plant width at soil surface of the low risk plants. Angle of root spread did not appear to influence these differences in root plate spread.

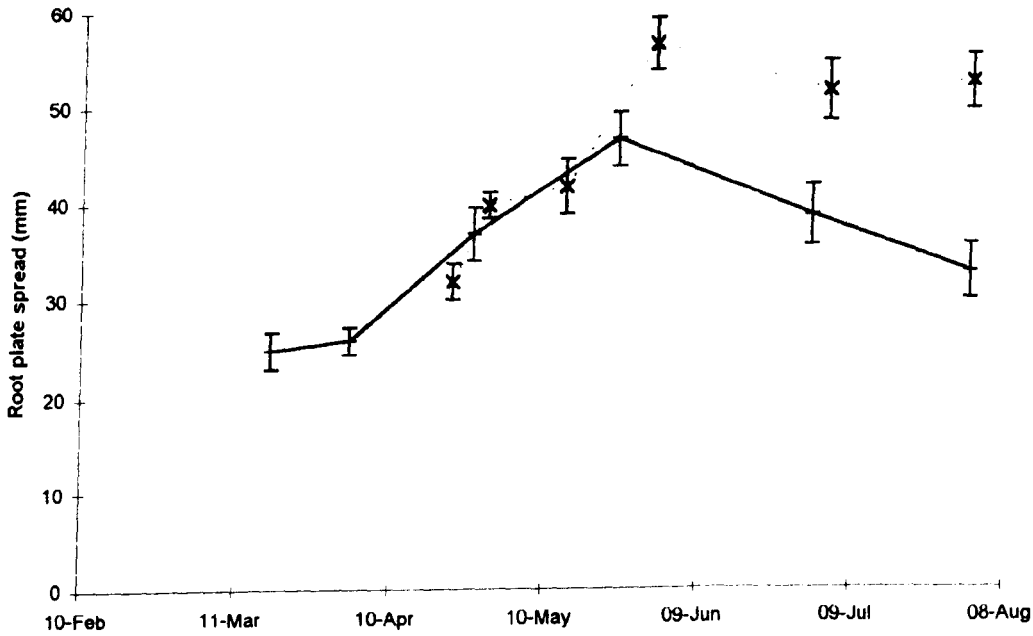

Figure 5.23 The development of root plate spread in the MT96 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

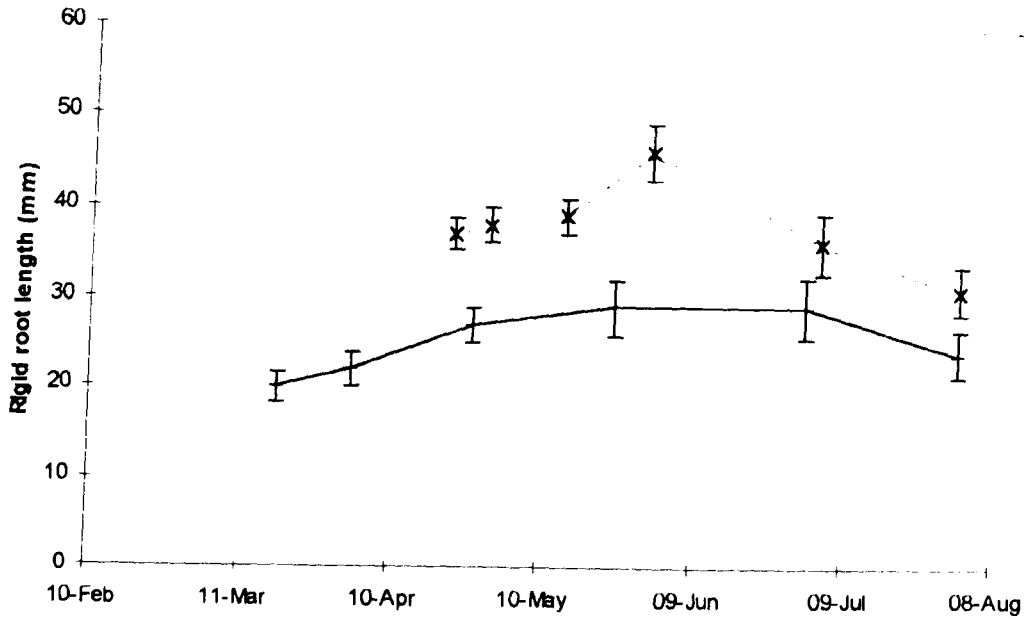

Figure 5.24 The development of rigid root length in the MT96 experiment growing season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

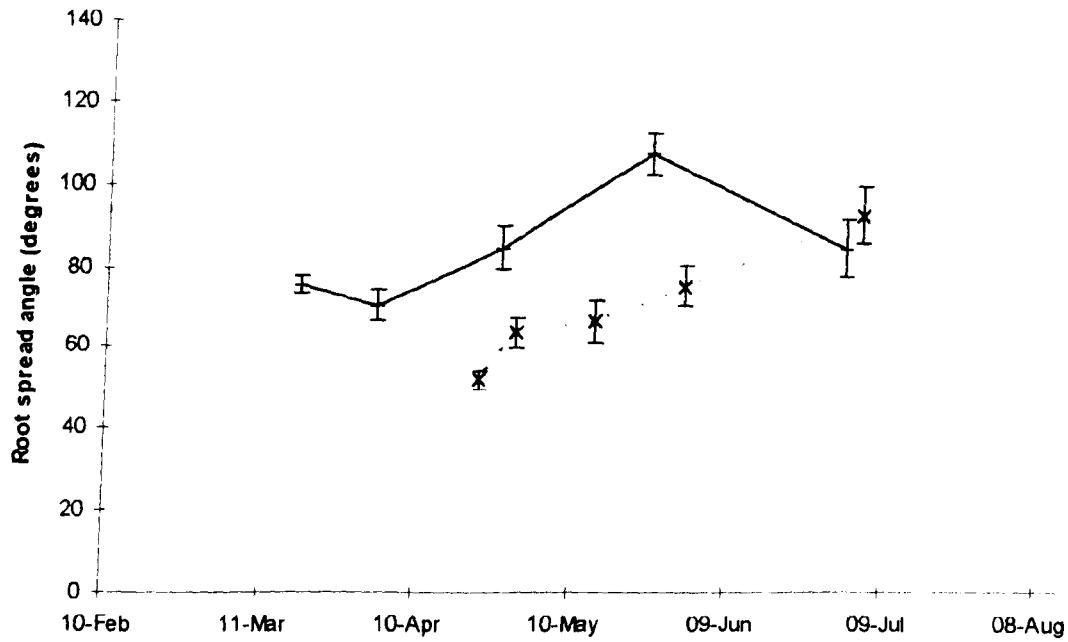

Figure 5.25 The development of the angle of root spread in the MT96 experiment growing season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

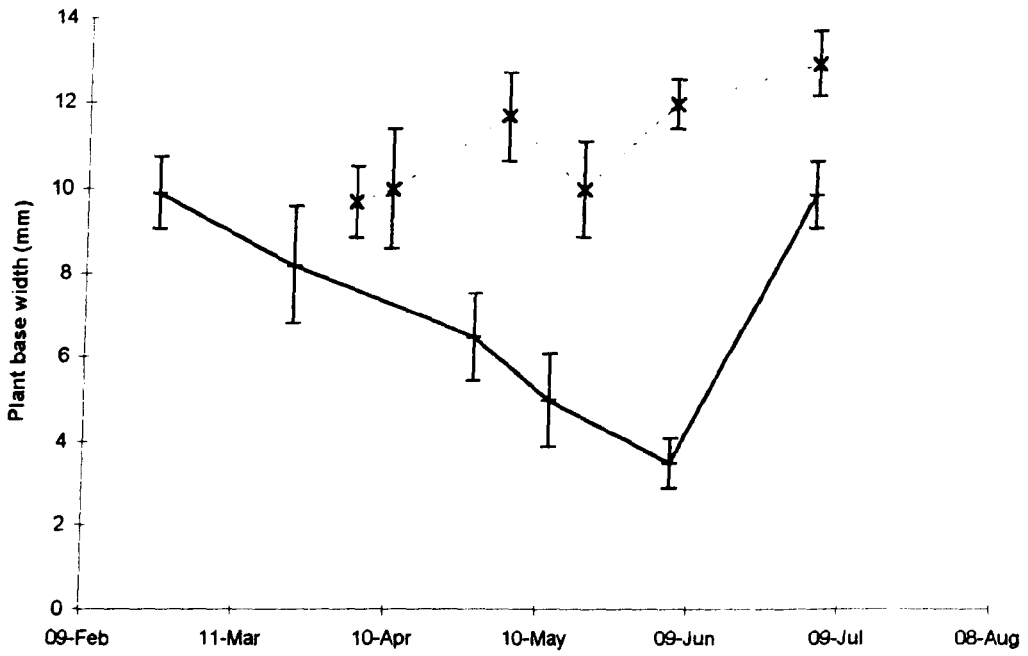

Figure 5.26 The development of the plant width at soil surface in the MT95 experiment growing season for the high (— + —) and low (- -×- -) risk treatments with PGRs. Bars represent ± SEM (23-56 df, see Appendix 5).

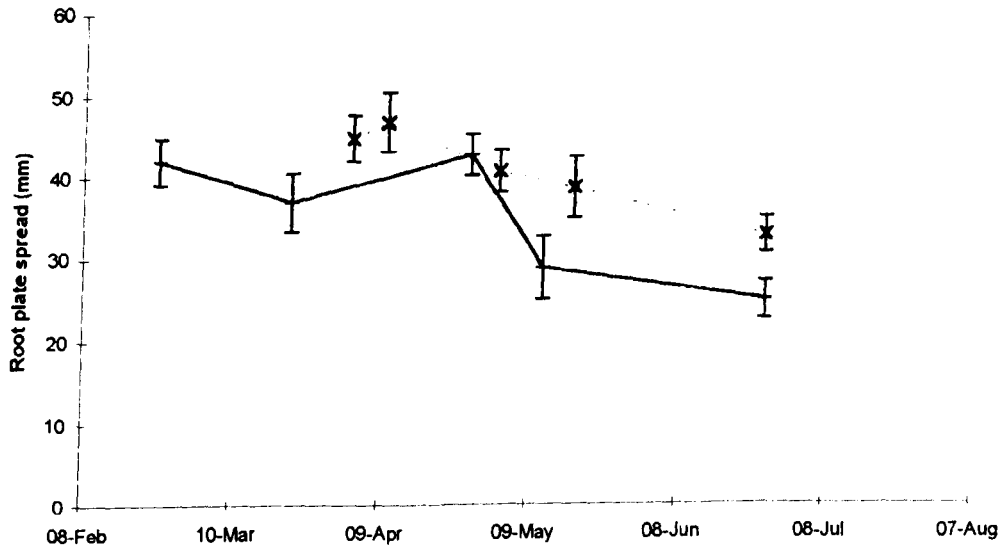

Figure 5.27 The development of root plate spread in the MT95 experiment growing season for the high (— + —) and low (- -×- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

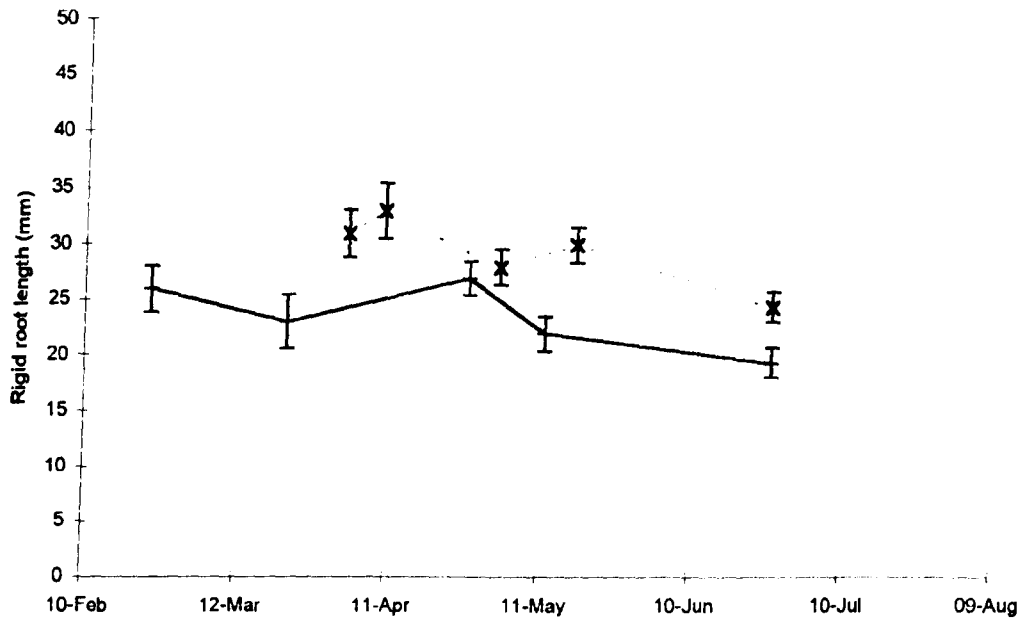

Figure 5.28 The development of rigid root length in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

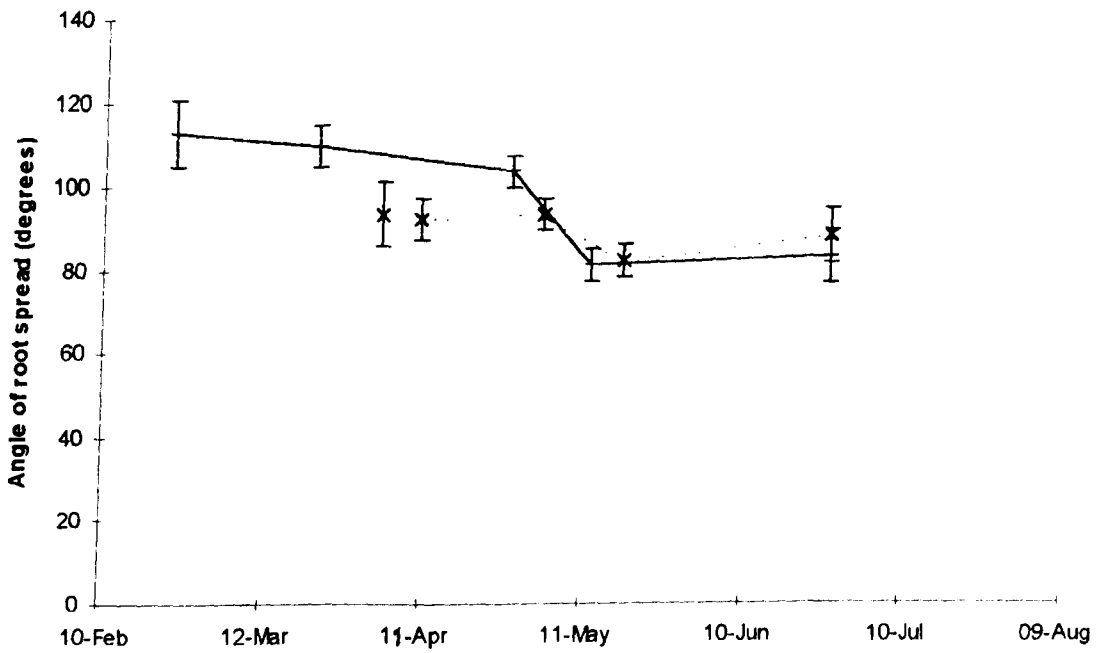

Figure 5.29 The development of the angle of root spread in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

The development of structural rooting depth in the MT96 experiment was erratic and associated with large SEMs (Figure 5.30). A paired t-test for the structural rooting depths of all treatments at GS 30 and at GS 71-73 in the MT96 experiment showed no statistically significant difference between the two data sets. In the MT95 experiment structural rooting depth decreased slightly between GS 30 and GS 69-71 (Figure 5.31). However, this observation may have been due to the difficult root extraction conditions in this season. No consistent differences in structural rooting depth were found between the high and low risk treatments in either experiment.

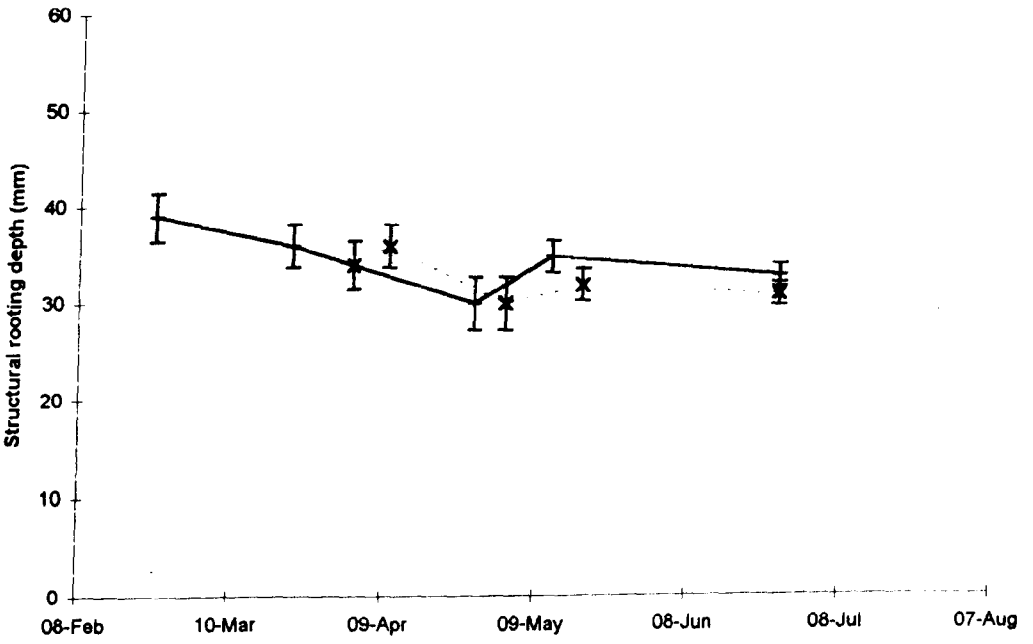

Figure 5.30 The development of structural rooting depth in the MT95 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

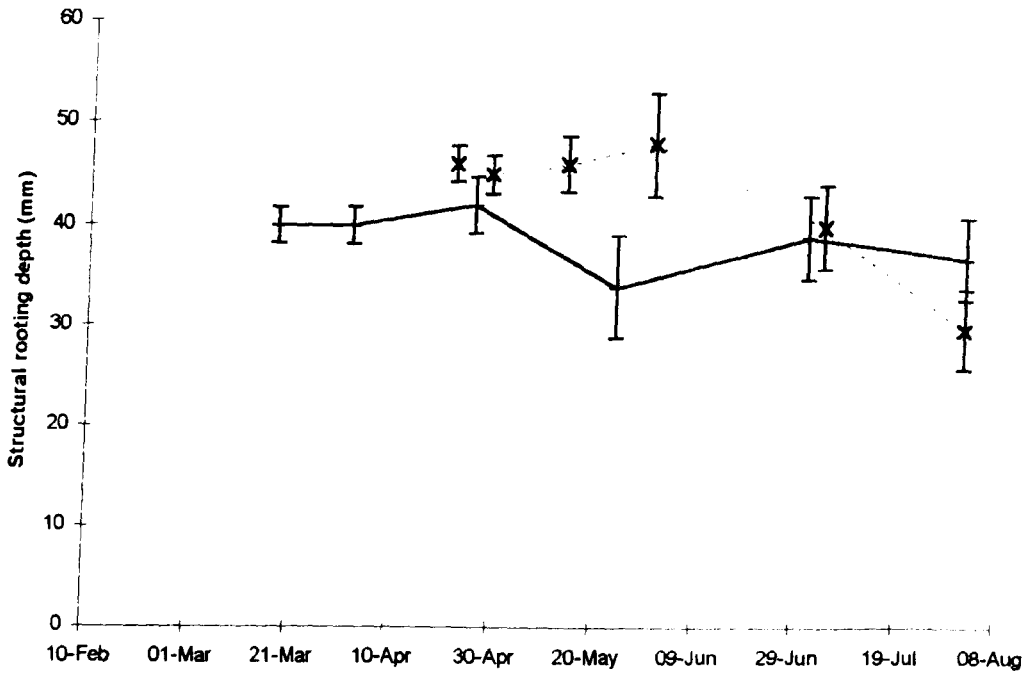

Figure 5.31 The development of structural rooting depth in the MT96 experiment growing season for the high (— + —) and low (- -x- -) risk treatments. Bars represent ± SEM (23-56 df, see Appendix 5).

5.4.2 The influence of variety

Root plate spread and structural rooting depth were measured at GS 31, GS 39 and GS 61 + 75 °Cd for five varieties (Figure 5.32 and Figure 5.33). There were statistically significant differences between these varieties for root plate spread at GS 31 ($P<0.001$) and GS 61 + 75 °Cd ($P<0.001$). Out of 21 varieties measured at the later growth stage, root plate spread ranged from 28 mm for Cadenza to 43 mm for Beaver. Between GS 31 and GS 61 + 75 °Cd there was no consistent trend in the size of root plate spread for the different varieties.

Large differences existed between the varieties for structural rooting depth at GS 31 ($P=0.068$), GS 39 ($P<0.05$) and GS 61 + 75 °Cd ($P<0.01$). Out of 21 varieties measured at the later growth stage these differences ranged from 32 mm for Soissons to 47 mm for Hereward. Structural rooting depth generally increased by between 2 and 10 mm from GS 31 to GS 61 + 75 °Cd. However, the varietal rankings for this plant character were not consistent between GS 31 and GS 61 + 75 °Cd.

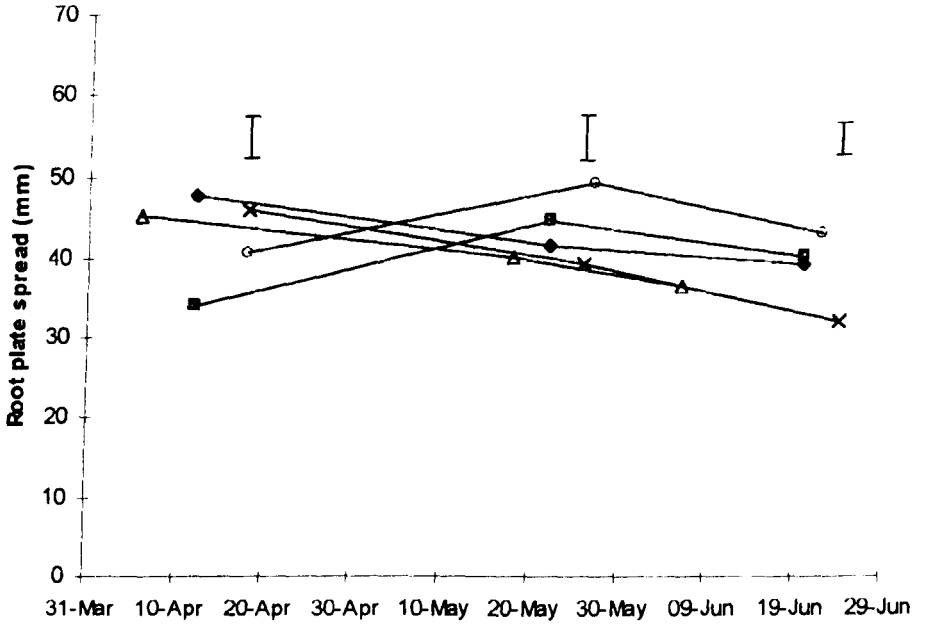

Figure 5.32 The development of root plate spread in the VT95 experiment for varieties. Riband (♦), Mercia (Δ),Hereward (■), Little Joss (×) and Beaver (○) Bars represent ± SEM (8 df).

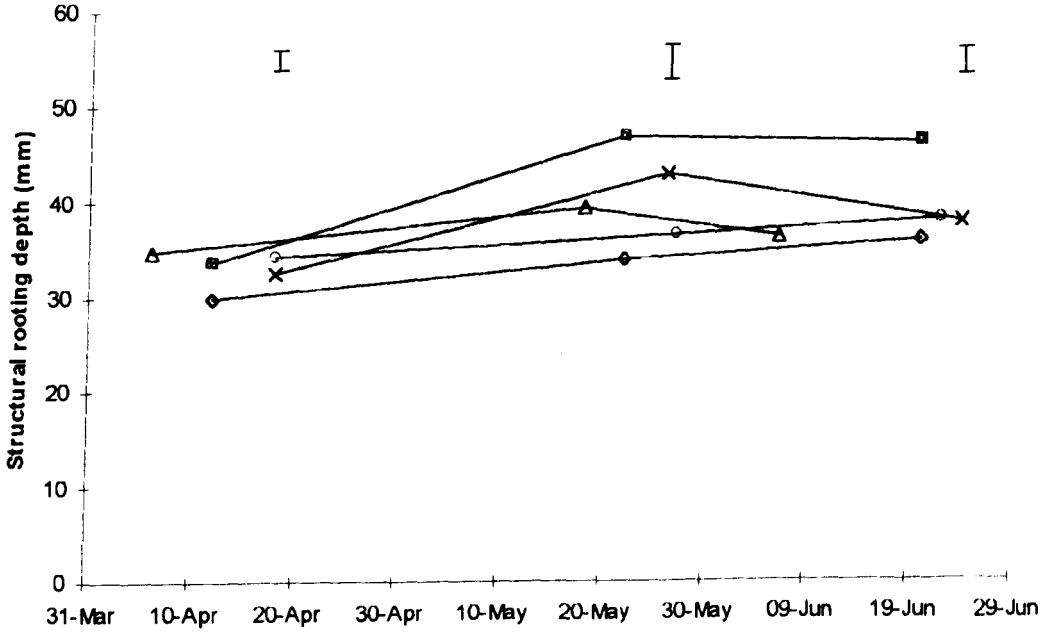

Figure 5.33 The development of structural rooting depth in the VT95 experiment for varieties Riband (♦), Mercia (Δ),Hereward (■), Little Joss (×) and Beaver (○). Bars represent ± SEM (8 df).

5.4.3 The influence of individual husbandry treatments

Seed rate

Seed rate had the greatest effect on root plate spread in both experiments (Table 5.16 and Table 5.17). Low seed rate significantly increased root plate spread ($P<0.001$) due to longer rigid root lengths and greater plant widths at soil surface. Angle of root spread was not affected by seed rate. In the MT96 experiment low seed rate resulted in an average root plate spread of 51 mm compared with only 44 mm for the high seed rate. When it is considered that anchorage failure moment is calculated from the root plate spread cubed, this difference becomes very significant.

Low seed rate significantly increased structural rooting depth in both experiments, probably by increasing rigid root length. At GS 71-73 in the MT96 experiment low seed rate resulted in an average structural rooting depth of 43 mm compared with only 38 mm for high seed rate. This seemingly small difference becomes more significant when the probabilities of receiving enough daily rain to saturate these depths (and severely weaken the soil) are considered. Based on long term weather data for July at ADAS Rosemaund, there is approximately a one in thirteen chance of receiving enough daily rain to bring 38 mm of silt clay loam soil from permanent wilting point to field capacity. This decreases to a one in twenty chance for a 43 mm soil depth.

Sowing date

Late sowing increased root plate spread in the MT95 experiment ($P= 0.094$) and the MT96 experiment ($P=0.059$). Despite being statistically non-significant the differences were as large as those found for seed rate, with late sowing causing an average root plate spread of 51 mm compared with only 43 mm for early sowing. These differences appeared to originate the late sowings causing significantly longer rigid roots ($P<0.05$). It is possible that the observed sowing date effect is similar to the seed rate effect, since the late sowings always had poorer establishment and fewer plants per metre squared.

In the MT95 experiment structural rooting depth was significantly increased by early sowing compared with late sowing at GS 33, 39 and 69-71 ($P<0.05$; Table 5.18). However, the difference was only 3 mm at GS 69-71. This effect was probably due to differences in crown depth. In both experiments crown depth at early sowing was significantly greater than at late sowing ($P<0.05$). In the MT95 experiment crown depth was increased from 13 mm to 20 mm at GS 30. In the MT96 experiment it was increased from 14 mm to 23 mm. Despite this, structural rooting depth was not increased by early sowing in the MT96 experiment (Table 5.19).

Residual nitrogen and lodging controls

Residual nitrogen and lodging controls had no statistically significant influence on root plate spread, structural rooting depth or their components in either experiment.

Table 5.16 Root plate spread (mm) at GS 69-71 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	24	28	26	36
soil	5C Cycocel (PGR)	29	27	26	34
residual	5C Cycocel + Terpal (PGR)	27	29	26	31
nitrogen	Canopy Management	24	32	26	38
Low	Nil spring lodging control	25	31	26	33
soil	5C Cycocel (PGR)	34	28	24	37
residual	5C Cycocel + Terpal (PGR)	24	30	27	34
nitrogen	Canopy Management	21	26	26	37

SED = 3.2 (56 df)

Table 5.17 Root plate spread (mm) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	39	45	46	59
residual	5C Cycocel (PGR)	40	42	47	50
nitrogen	Canopy Management	44	42	46	52
Low soil	Nil spring lodging control	40	56	51	53
residual	5C Cycocel (PGR)	39	47	47	54
nitrogen	Canopy Management	36	50	48	57

SED = 4.5 (40 df)

Table 5.18 Structural rooting depth (mm) at GS 69-71 for the MT95 experiment.

Treatments		23 September sowing		19 October sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High	Nil spring lodging control	32	33	28	32
soil	5C Cycocel (PGR)	35	32	28	31
residual	5C Cycocel + Terpal (PGR)	32	35	29	29
nitrogen	Canopy Management	32	28	35	33
Low	Nil spring lodging control	33	34	27	30
soil	5C Cycocel (PGR)	32	32	28	32
residual	5C Cycocel + Terpal (PGR)	35	34	29	31
nitrogen	Canopy Management	31	31	28	32

SED = 1.7 (56 df)

Table 5.19 Structural rooting depth (mm) at GS 71-73 for the MT96 experiment.

Treatments		20 September sowing		1 November sowing	
		500 seeds m^{-2}	250 seeds m^{-2}	500 seeds m^{-2}	250 seeds m^{-2}
High soil	Nil spring lodging control	41	44	43	40
residual	5C Cycocel (PGR)	40	42	37	40
nitrogen	Canopy Management	42	43	33	37
Low soil	Nil spring lodging control	42	45	42	46
residual	5C Cycocel (PGR)	35	38	31	44
nitrogen	Canopy Management	40	43	31	45

SED = 4.6 (40 df)

5.4.4 Summary

Values of root plate spread increased from GS 30 onwards, due to lengthening rigid roots and widening angle of root spread, before stabilising at around GS 39. Large differences were observed between the high and low risk treatments from GS 30 onwards, which suggests that potential variation in root plate spread can be identified early enough for remedial action to be taken. Genotypic differences in root plate spread were slightly smaller than the husbandry differences, which were caused by seed rate and sowing date. The seed rate and sowing date effects appeared to result from differences in plant population, which had an inverse relationship with root plate spread.

Structural rooting depth did not change from GS 30 onwards in the husbandry experiments. This was surprising since rigid root length did increase over this time period. In the VT95 experiment structural rooting depth demonstrated the expected increase from GS 30 onwards, with the actual increase depending on variety. Unlike root plate spread, genotypic variation in structural rooting depth was greater than variation due to husbandry. Low seed rate and early sowing increased rooting depth due to longer rigid roots and deeper crowns respectively.

5.5 PREDICTING THE LODGING-ASSOCIATED PLANT CHARACTERS

The aim of the next chapters is to develop and test prediction schemes for the July values of each plant character starting with measurements taken at the beginning of stem extension (GS 30). It is apparent that the task of developing such prediction schemes for a group of diverse plant characters which encompass all aspects of the wheat plant and which are all influenced by season, genotype and husbandry is considerable. Therefore, it appears sensible to prioritise the plant characters for which prediction schemes will be developed. The value of this study will be maximised by selecting the plant characters for which a prediction scheme will offer the most effective assessment of lodging risk.

5.5.1 The value of each prediction scheme

The value of developing a particular prediction scheme depends on a number of factors:

1. Probably the most important. The sensitivity of lodging to typical variation in the plant character. The more it affects lodging, the greater the need for an accurate prediction scheme.

2. Have the plant characters in question formed by GS 30 ? (e.g. a true stem does not exist at GS 30, therefore its properties cannot be measured) If not, then prediction schemes must be based on substitute plant characters.

3. If a plant character to be predicted has formed by GS 30, does its value change between GS 30 and the time of high lodging risk? If it does, then this must be accounted for in the prediction scheme.

4. Does the plant character change due to site, growing season, husbandry or genotype? If it does, then a prediction scheme must account for this variation.

To gauge the sensitivity of lodging due to variation in each plant character, a parametric investigation has been carried out (Table 5.20). This illustrates how much a component of lodging can be altered by the plant characters used in its calculation. The range of each lodging-associated plant character has been taken from the MT95, MT96 and VT95 experiments and is shown in Table 5.20. The methods described in Baker *et al.* (Appendix 1) have been used with a daily rainfall of 5 mm and a maximum wind gust of 13 m s^{-1} to calculate the components of lodging. These give default values of 41 Newton millimetres (Nmm) for shoot base bending moment, 123 Nmm for plant base bending moment, 85 Nmm for stem failure moment and 183 Nmm for anchorage failure moment.

Table 5.20 Sensitivity of the lodging components to the plant characters used in their calculation.

Plant character	Experimental range	Standard value (Baker *et al.*; Appendix 1)	Sensitivity of lodging component
			Shoot base bending moment
Height at centre of gravity	32 to 61 cm	50 cm	31 to 47 Nmm
Natural frequency	0.5 to 1.4 Hz	1 Hz	74 to 34 Nmm
			Plant base bending moment
Shoot number per plant	1.7 to 5.7	3	69 to 233 Nmm
			Stem failure moment
Stem diameter	2.6 to 4.8 mm	3.0 mm	59 to 264 Nmm
Stem wall width	0.4 to 0.9 mm	0.5 mm	76 to 104 Nmm
Failure yield stress	30 to 70 MPa	40 MPa	66 to 149 Nmm
			Anchorage failure moment
Root plate spread	17 to 58 mm	35 mm	21 to 834 Nmm
[1] Structural rooting depth	27 to 50 mm	35 mm	160 to 210 Nmm

[1] This character has a small direct effect on anchorage failure moment. It affects this character mainly by influencing the likelihood of soil receiving enough rainfall to wet up and weaken it, this is described in more detail below.

Table 5.20 shows that typical variations in root plate spread, stem diameter and shoot number per plant cause the greatest changes in the lodging components which they influence, with changes greater than threefold. Variation in stem failure yield stress and natural frequency cause about a twofold difference in stem failure moment and shoot base bending moment respectively. Variation in height at centre of gravity, stem wall width and structural rooting depth cause the least variation in the lodging components which they influence. At this point it should be noted that this parametric investigation is artificial in that it is known that there are many interactions between the chosen parameters. This parametric analysis merely helps by identifying those parameters having the largest effect on the lodging components.

Structural rooting depth exerts its main effect on lodging by affecting the amount of rainfall needed to wet up and weaken the soil. The probability of receiving enough daily rain to wet the deepest rooting depth (Table 5.20) from permanent wilting point to field capacity is about 0.03. This compares to a probability of only 0.14 to wet up the shallowest rooting depth. When it is considered that wetting a soil from permanent wilting point to field capacity may reduce the soil strength (and anchorage strength) by ten fold, it is apparent that structural rooting depth will have a large effect on lodging risk. Therefore, the value of a prediction scheme for this character is likely to reasonably significant.

A description of the four points required to assess the value of a prediction scheme for each plant character is given in Table 5.21. This table also acts as a summary of the main findings in Chapter 5. Only shoot number per plant, root plate spread and structural rooting depth have formed by GS 30, which is the time by which most decisions for lodging control must be taken. In the MT95 and MT96 experiments structural rooting depth showed little change from GS 30 onwards. Although this was not supported in the VT95 experiment, it is possible that the summer-time structural rooting depth could be predicted simply from measurements at GS 30. Shoot number per plant and root plate spread continue to change after GS 30, with final shoot number per plant stabilising at around anthesis and root plate spread

stabilising at GS 39. Prediction of these plant characters may be based on GS 30 values, but must account for these changes. At GS 30 the other plant characters have not developed sufficiently (formed) to allow measurement. Therefore, prediction schemes will be necessary which are based on substitute plant characters measured at GS 30. Finally, the knowledge that root plate spread and stem failure yield stress have stabilised by GS 39 could be useful when considering late remedial action, which can be administered as late as GS 45.

All the plant characters differed due to two of season, variety and husbandry. Shoot number per plant was evidently the most variable plant character, being much affected by variety and husbandry and also affected by season. All plant characters showed at least moderate variation due to genotype, thus demonstrating the importance of this factor. It appears that most prediction schemes will have to take account of variation due to genotype and husbandry. However, it should be noted that more seasons and sites must be studied to fully illustrate how these factors influence the plant characters.

Finally, stem diameter, shoot number per plant and root plate spread have the largest effect on the lodging components; stem failure yield stress, natural frequency and structural rooting depth have a medium influence; and stem wall width and height at centre of gravity have a small influence. It appears that only structural rooting depth may not require a prediction scheme, depending on whether or not it changes after GS 30. All other plant characters require a prediction scheme because their final value is not set until after GS 30. In addition they are all affected by two or more factors. For these reasons the values of the prediction schemes (Table 5.21) are primarily based on their influence on the components of lodging.

Table 5.21 A description of the lodging-associated plant characters with a view to prediction.

Plant character	Growth stage after GS 30 when character is first formed	Earliest date when final value is set	Variation between seasons	Variation due to variety	Variation due to husbandry	Influence on its lodging component (From Table 5.20)	Value of a GS 30 - harvest prediction
Stem diameter	GS 33	Harvest	Low	Moderate	Moderate	Large	Large
Stem wall width	GS 33	Harvest	Low	Moderate	Moderate	Small	Small
Stem failure stress	GS 33	GS 39	Moderate	High	Low	Medium	Medium
Natural frequency	GS 39	Harvest	Low	Moderate	Moderate	Medium	Medium
Height at centre of gravity	GS 39	Harvest	Low	Moderate	Moderate	Small	Small
Shoot number per plant	GS 30	GS 61	Moderate	High	High	Large	Large
Root plate spread	GS 30	GS 39	Moderate	Moderate	Moderate	Large	Large
Structural rooting depth	GS 30	GS 30/39?	Moderate	Moderate	Low	Medium	none/Medium

Plasticity ratings
High - > 100% variation between the extreme values
Moderate - < 100% & > 25%
Low - < 25%

5.5.2 The general form of prediction schemes

This study will be of greatest value to the wheat grower by developing prediction schemes for root plate spread, stem diameter and shoot number per plant. Therefore the majority of the following three chapters concerns the development and testing of prediction schemes for these plant characters. The significance of the other lodging-associated plant characters is recognised and these are dealt with less rigorously. Chapter 6 deals with the plant characters used to calculate anchorage failure moment, with emphasis given to root plate spread. Chapter 7 deals with the plant characters used to calculate stem failure moment, with emphasis directed towards stem diameter. Chapter 8 deals with the plant characters used to calculate shoot and plant base bending moment, with the emphasis on shoot number per plant. This order has been chosen because it appears from Table 5.21 that a prediction scheme for root plate spread will be most valuable, followed by stem diameter, followed by shoot number per plant. However, it should be recognised that these conclusions are based on limited data.

Where possible, prediction schemes are based entirely on scientific literature, which will allow them to be tested in the lodging experiments. However, whilst substantial information exists for most of the lodging-associated plant characters, some have been studied very little. In such cases, data from the lodging experiments have been used to develop the prediction scheme. This precludes the testing of such schemes in the present study. Investigations in this chapter have shown that all the lodging-associated plant characters were significantly influenced by genotype. However, the general patterns of development and growth were usually similar between varieties. Therefore, the following prediction schemes will be developed or tested with data from the husbandry experiments involving Mercia only. It is anticipated that further work on varieties may be required to calibrate the prediction schemes to suit individual varieties.

6. PREDICTING ANCHORAGE FAILURE MOMENT

It was concluded in Chapter 5 that the development of a prediction scheme for root plate spread was extremely important. This was due to its very large influence on anchorage strength and its continued development after GS 30. The development of a prediction scheme for structural rooting depth was relatively less important. There was even an indication that a prediction of this character would not be needed as values measured at GS 30 were often similar to values at the time of lodging. However, this was uncertain.

The structural rooting characters, root plate spread and structural rooting depth, are relatively new parameters; they have been subjected to little previous research. From the small amount of evidence about these characters in the scientific literature it is difficult to develop prediction schemes which link spring-time observations with their summer-time values. Therefore the experiments of the 'Lodging Project' have been used to develop understanding of these structural root characters and to formulate prediction schemes. It must be emphasised that data from the experiments of the 'Lodging Project' cannot be used to test such prediction schemes; it would be the remit of further work to carry out validation tests.

The diagram of the base of a wheat plant (Figure 2.1) indicates that root plate spread and structural rooting depth are influenced by a number of components. Root plate spread is expected to be a function of rigid root length, plant base width and the angle of root spread. Structural rooting depth is expected to be a function of crown depth, rigid root length and the angle of root spread. The investigations of Chapter 5 indicated that variation in root plate spread and structural rooting depth resulted from variation in some components more than others. If the components which caused the most variation in root plate spread and structural rooting depth can be identified, prediction schemes may be developed for these important components which will help predict root plate spread and structural rooting depth.

The diagram of the base of a wheat plant (Figure 2.1) indicates that the structural root characters will relate through simple geometry. This has been investigated in the MT95, MT96 and VT95 experiments by comparing the observed relationships with expected geometrical relationships. This indicated the importance of each component in terms of the amount of variation in root plate spread or structural rooting depth it caused. The influence of genotype has been included in this preliminary investigation because it will provide valuable information if the prediction schemes set up in this thesis (for Mercia only) are calibrated for other varieties' in future work.

6.1 ROOT PLATE SPREAD

6.1.1 Understanding root plate spread

Root plate spread and rigid root length were significantly correlated in both the husbandry and variety experiments ($P<0.01$; Figure 6.1 and Figure 6.2), such that a longer rigid root length was associated with a greater root plate spread. Rigid root length accounted for about 70% of the variation in root plate spread in both experiments. The slope of the best fit lines were similar to that expected if geometrical principles were used to calculate root plate spread from rigid root length assuming an angle of root spread of 90°. It seems likely that the spread of the root plates predicted from rigid root length in the experiments were slightly smaller than those predicted by the expected relationship, because the average experimental angle of root spread was less than 90°. The intercept of the best fit line would be expected to be zero, or if the plant base width is assumed to be important, greater than zero. The experiments gave an intercept which was slightly negative. In the MT95 and MT96 experiments this may have resulted from combining the two seasons, since when each season is analysed individually a positive intercept is found.

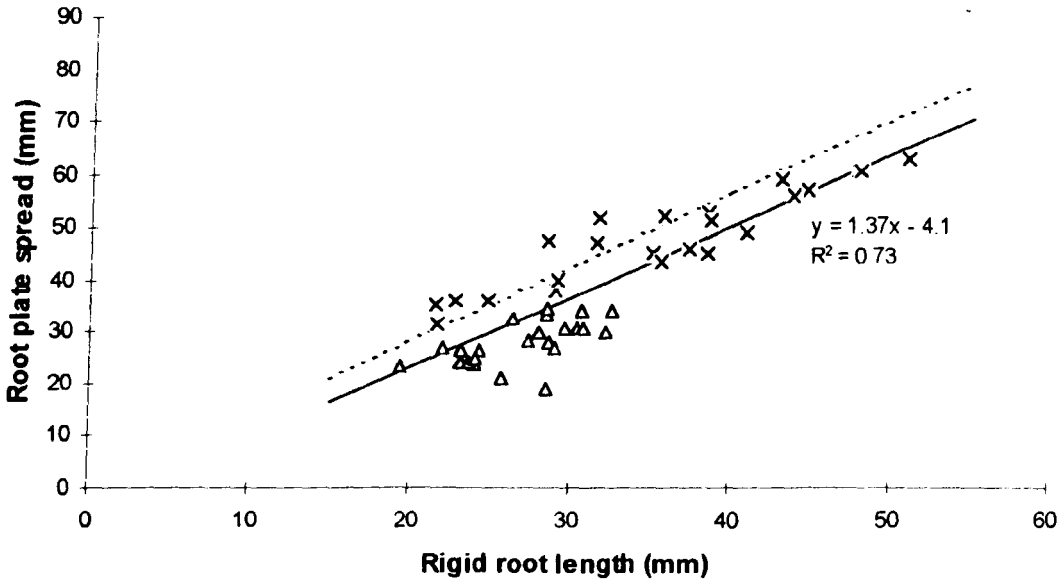

Figure 6.1 Rigid root length plotted against root plate spread at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The expected geometrical relationship (---) assumes an angle of root spread of 90°. The best fit line (—) is for MT95 and MT96 is given.

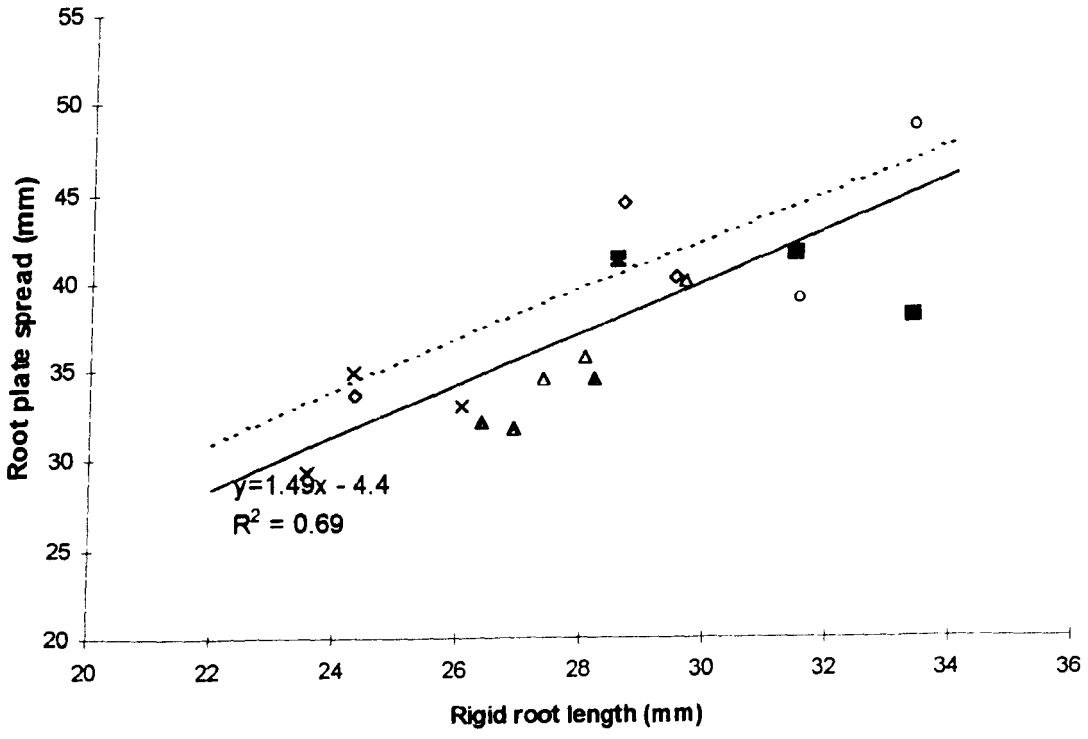

Figure 6.2 Rigid root length plotted against root plate spread at GS 61 + 75 °Cd for Riband (◇), Mercia (Δ),Hereward (■), Little Joss (×), Beaver (○) and Apollo (▲). The expected geometrical relationship (---) assuming an angle of root spread of 90° and best fit line (—) are shown.

A greater root plate spread was associated with a greater angle of root spread in the MT95 and VT95 experiments ($P<0.05$; Figure 6.3 and Figure 6.4). The best fit lines were similar in gradient to that expected if geometrical principals were used to calculate root plate spread from angle of root spread, if a rigid root length of 30 mm is assumed. The best fit line in MT95 had a smaller intercept because the average rigid root length of this experiment was smaller than that used in the expected relationship. It seems likely that angle of root spread has a small influence on root plate spread, as it accounted for only 37 to 45 % of the variation in root plate spread in MT95 and VT95. In addition, no statistically significant relationship was found between these two plant characters in the MT96 experiment (Figure 6.3).

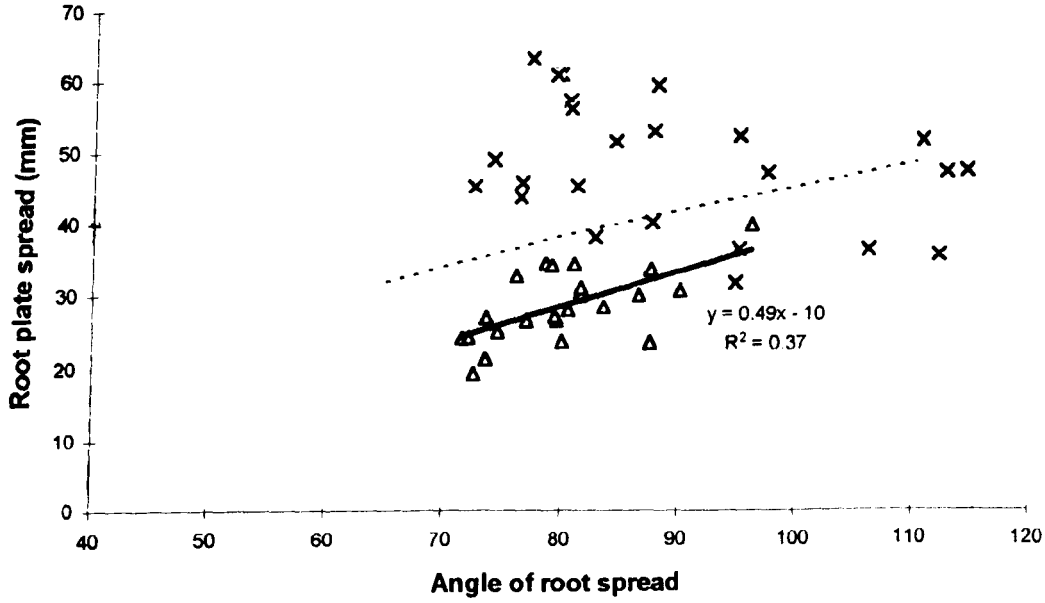

Figure 6.3 Angle of root spread plotted against root plate spread at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The expected geometrical relationship (---) assuming a rigid root length of 30 mm and best fit line (—) for MT95 are shown.

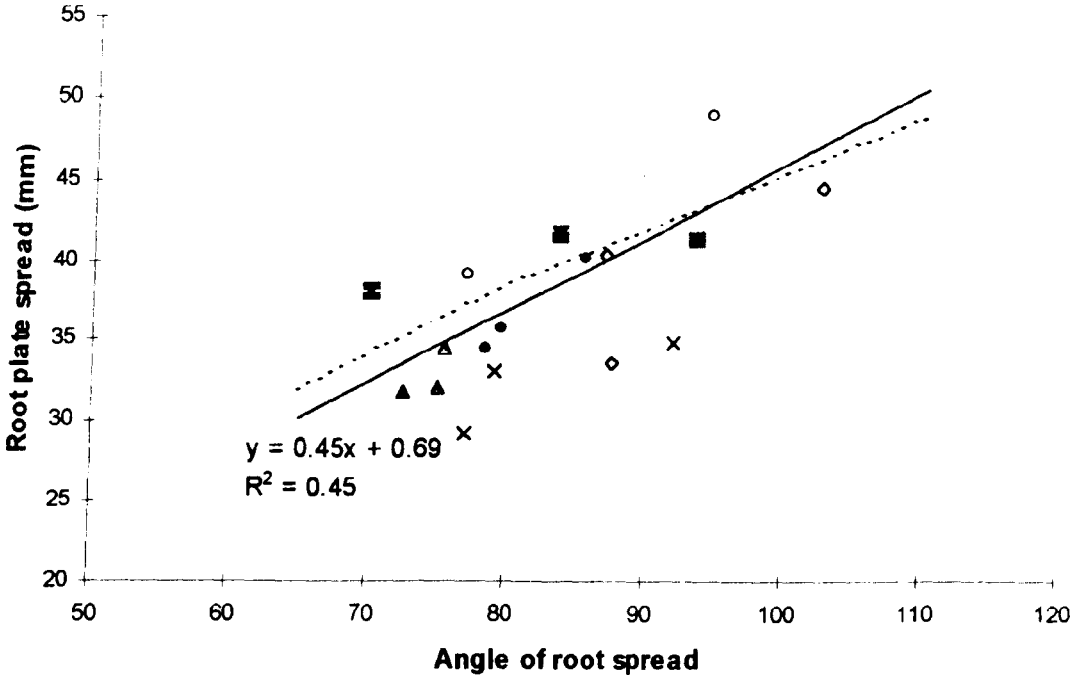

Figure 6.4 Angle of root spread plotted against root plate spread at GS 61 + 75 °Cd for Riband (◇), Hereward (■), Little Joss (×), Beaver (○) and Apollo (▲). The expected geometrical relationship (---) assuming a rigid root length of 30 mm and best fit line (—) are shown.

The width of the plant base was positively related with root plate spread in the MT95 and VT95 experiments ($P<0.05$; Figure 6.6 and Figure 6.7). The best fit lines showed a similar gradient to the 1:1 relationship which suggests that unit increases in plant width at soil level caused similar unit increases in root plate spread. Changes in plant width at soil level in the MT95 husbandry experiments accounted for a large proportion (59 %) of the variation in root plate spread. In the variety experiments only 32 % of the variation was accounted for. Plant width at soil level was not measured in the MT96 husbandry experiment.

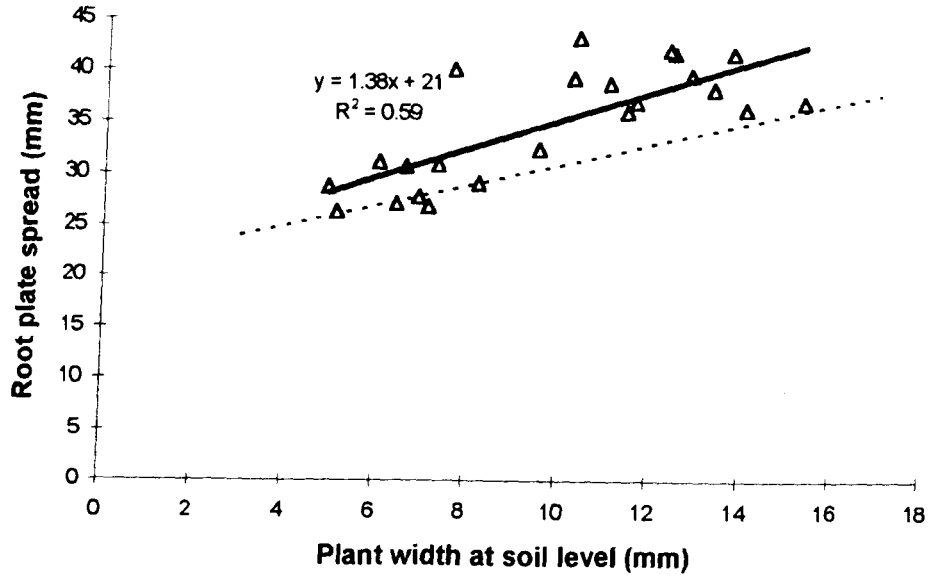

Figure 6.5 Plant width at soil level and crown width plotted against root plate spread at GS 39 for the MT95 (Δ) experiment. The 1:1 relationship (---) and best fit line (—) are shown.

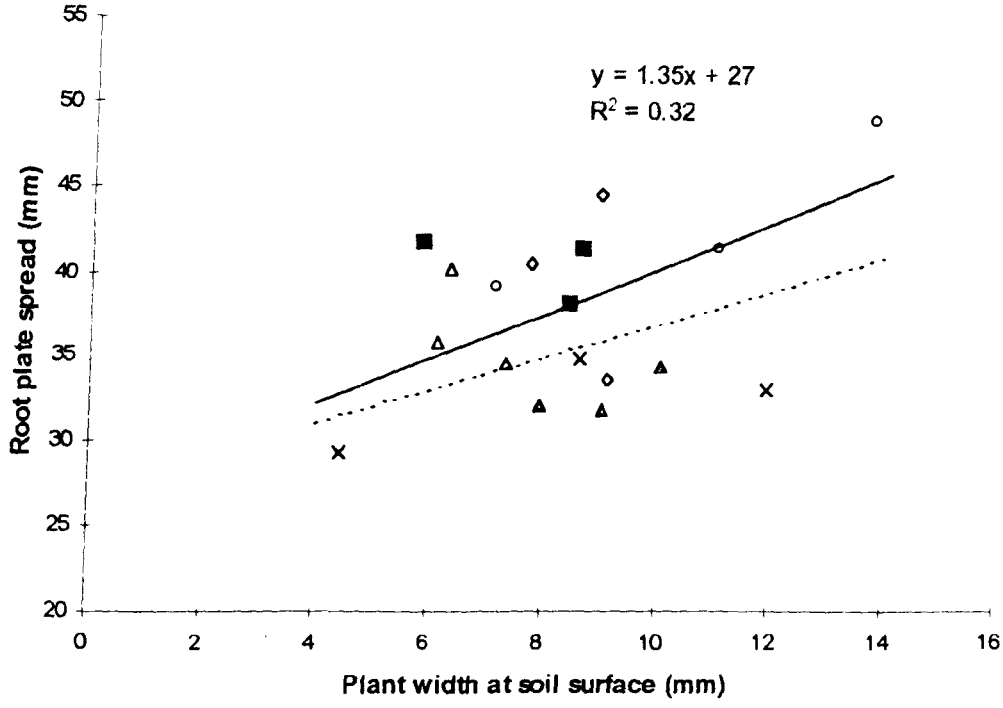

Figure 6.6 Plant width at soil level plotted against root plate spread at GS 61 + 75 °Cd for Riband (◇), Mercia (Δ),Hereward (■), Little Joss (×), Beaver (○) and Apollo (▲). The 1:1 relationship (---) and best fit line (—) are shown.

6.1.2 Predicting root plate spread

Root plate spread can be measured as early as GS 30. Therefore, the first investigation should be whether spring measurements of root plate spread might be used to predict summer-time values because this would be the most straight forward prediction. No statistically significant relationship was found between root plate spread measured at GS 30 and GS 69-71 in the MT95 and MT96 experiments (Figure 6.7). It appears that early season differences in root plate spread were not maintained until summer. These results indicate that the summer-time values of root plate spread cannot be accurately predicted from its spring-time measurements.

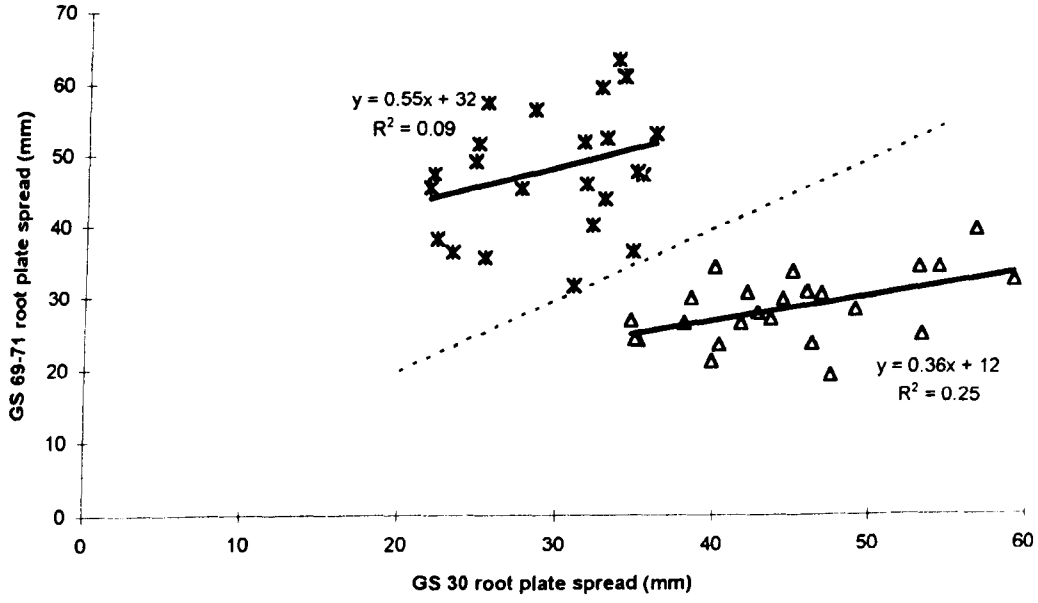

Figure 6.7 Root plate spread measured at GS 30 plotted against root plate spread at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The 1:1 relationship (---) and best fit lines (—) are shown.

An alternative method of predicting root plate spread must be sought. It has been shown that variation in root plate spread due to genotype or husbandry was mainly due to changes in rigid root length. Plant base width and angle of root spread had a smaller influence. Therefore, it is likely that predicting rigid root length would help predict root plate spread.

Low density plant populations have crown roots with a greater diameter and bending moment (Easson *et al.*, 1995), which suggests that rigid root length will be influenced by plant density. It seems likely that this effect was due to the plants shade avoidance mechanism. Wheat plants grown in poor light quality, as often found in dense plant populations, have a smaller shoot biomass (due to fewer tillers) but a greater shoot:root ratio (Kasperbauer and Karlen, 1986; Knauber and Banowetz, 1992). It appears that plants growing in dense populations (shaded conditions) invest proportionally more assimilate in the shoots compared with the roots, to enable rapid growth away from the detrimental conditions (Kasperbauer and Karlen, 1986). A smaller assimilate supply to the root system is likely to cause thinner weaker roots with a shorter rigid length. Plant population density is also expected to affect plant base width, which was positively related to root plate spread. Plants of low population densities are usually associated with a greater number of shoots per plant (Darwinkel, 1978). This response may also result from the plants shade avoidance tactics (Kasperbauer and Karlen, 1986), and would be expected to increase the width of the plant base. Neither Pinthus (1967) nor Belford *et al.* (1986) found angle of root plate spread to be influenced by plant density or row width. This study found angle of root spread was the least influential component of root plate spread. It seems likely that plant density influences two important components of root plate spread and may therefore determine root plate spread itself. This has been investigated in the experiments with the aim of using spring plant density to predict root plate spread.

The effect of plant density on rigid root length has been investigated in the MT95 and MT96 experiments (Figure 6.8). There was a statistically significant relationship between spring plant number and rigid root length measured at the beginning of grain filling in both experiments ($P<0.01$). Smaller plant densities were associated with longer rigid root lengths. A strong negative relationship was also found between plant base width and plant number ($P<0.001$; Figure 6.9). This suggests that plant density will be inversely related to root plate spread. In agreement with previous

research, no evidence was found for angle of root spread to be influenced by the density of plants in the MT95 or MT96 experiments (Figure 6.10).

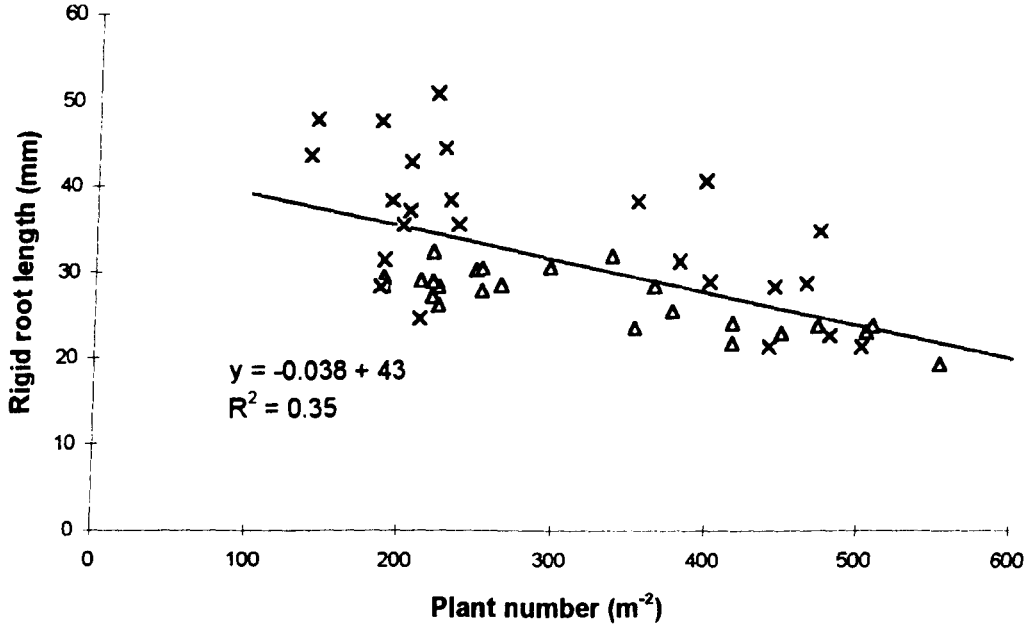

Figure 6.8 Spring plant population plotted against rigid root length measured at GS 69-73, for the MT95 (Δ) and MT96 (×) husbandry experiments. The best fit line (—) is shown.

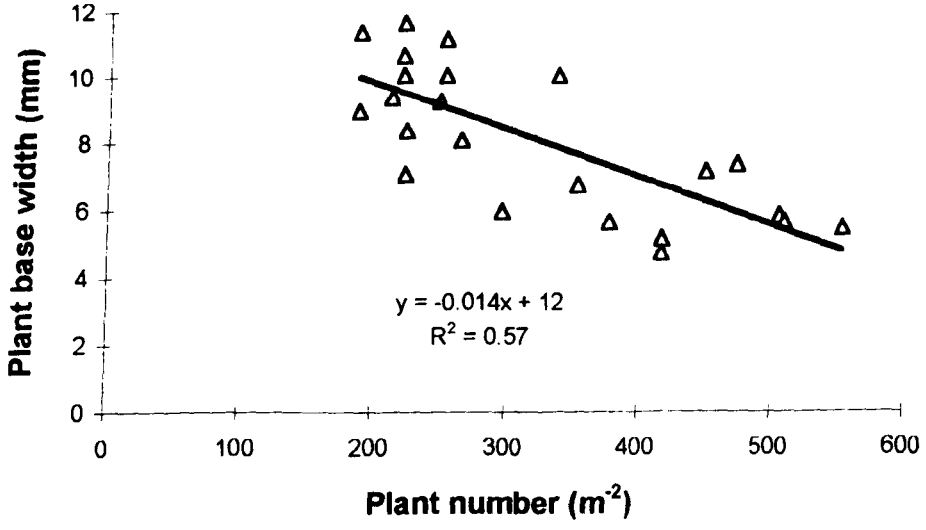

Figure 6.9 Spring plant population plotted against plant base width measured at GS 69, for the MT95 (Δ). The best fit line (—) is shown.

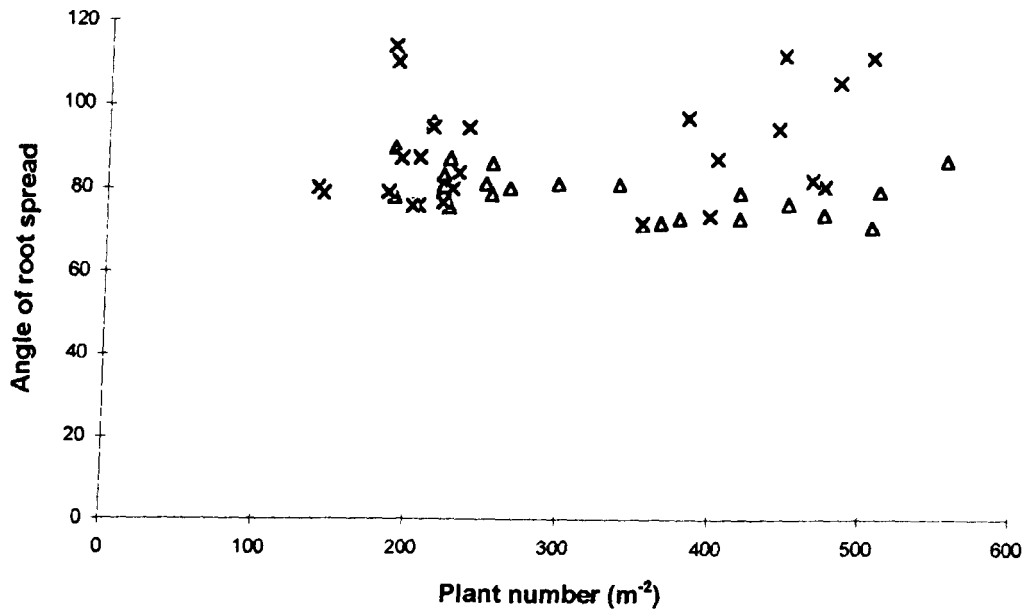

Figure 6.10 Plant population plotted against angle of root spread at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments.

The two most important components of root plate spread (rigid root length and plant base width) were strongly influenced by spring plant number, suggesting that spring plant number will give a good indication of root plate spread. The husbandry experiments have shown that root plate spread is related to plant population density ($P<0.01$), with smaller plant populations resulting in greater root plate spreads (Figure 6.11). This relationship varied between seasons, with the line of best fit for the MT95 experiment having a shallower gradient which crossed the Y axis at a smaller root plate spread in comparison with the MT96 experiment. It was suggested in Chapter 5 that dry soil conditions during the 1995 summer caused incomplete root extraction in the MT95 experiment, which resulted in the root plate spread appearing to diminish between spring and summer. It was concluded that the pattern of development of this season was not typical and conclusions about the structural rooting characters should be drawn mainly from the MT96 experiment. For these reasons the equation relating spring plant number m^{-2} and root plate spread during grain filling for the MT96 experiment (Figure 6.11) will form the empirical prediction of root plate spread (Equation 6.1).

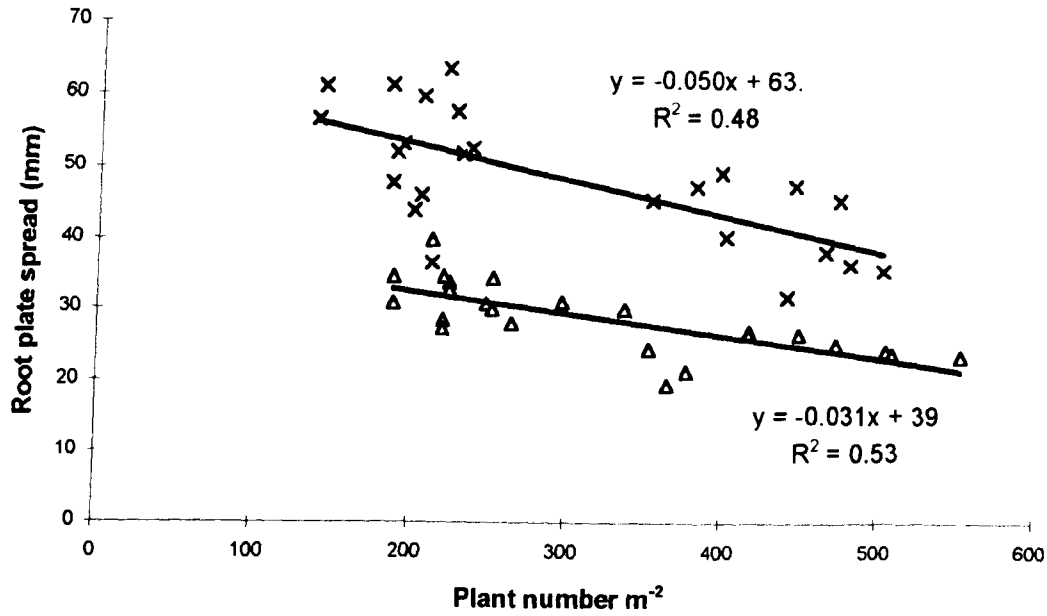

Figure 6.11 Plant population plotted against root plate spread measured at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The best fit lines (—) are shown for each experiment.

$$D = -0.05P + 63 \qquad \textbf{Equation 6.1.}$$

D - root plate spread (mm) in July

P - plant number (m^{-2}), measured in autumn

This equation calculates that plants from a sparse population, of 100 plants m^{-2}, would have a root plate spread of 58 mm and plants from a dense population, of 500 plants m^{-2}, would have a root plate spread of 38 mm. It is apparent that this variation in plant population density will have a very large effect on anchorage because root plate spread is cubed in the calculation of anchorage strength.

6.1.3 Conclusions

The scientific literature provides evidence for two important components of root plate spread, rigid root length and the width of the plant base, to be inversely related to plant density. It seems likely that the plant's shade avoidance tactics caused these relationships. These experiments have demonstrated that spring plant population density can account for differences in the summer-time root plate spread reasonably well. However, it must be noted that this prediction scheme has been developed from one site, in one season, and for one variety. It is recognised that further testing will be required to validate the prediction scheme for this very important plant character. For example, it has been shown in Chapter 5 that genotype plays a large role in determining the size of the root plate spread. Different genotypes would be expected to respond to different plant densities in a similar way as found for Mercia, but it is likely that the intercept, or/and gradient of equation 6.1 will change for each variety. These changes should be investigated and quantified in future work.

An explanation is required as to why GS 30 measurements of root plate spread did not account for differences later in the season. This was an unexpected result when it is considered that similar treatment differences in root plate spread were present at GS 30 and at GS 69-73. It appears to be the high variability of this plant character which prevents early season measurements relating well with late season measurements. If this plant character can be measured more precisely, perhaps by measuring more plants, then a prediction scheme which is based on GS 30 measurements of root plate spread might be developed.

6.2.1 Understanding structural rooting depth

The most important components of structural rooting depth are expected to be crown depth, rigid root length and angle of root spread. Changes in crown depth were not associated with variation in structural rooting depth in the MT95 and MT96 experiments (Figure 6.12). In the VT95 experiment crown depth strongly influenced the structural rooting depth, with greater crown depths associated with greater structural rooting depths ($P<0.001$; Figure 6.15). These genotypic changes in crown depth accounted for 61% of the variation in structural rooting depth. The best fit line showed a similar gradient to the 1:1 relationship which suggests that unit increases in structural rooting depth were caused by unit increases in crown depth.

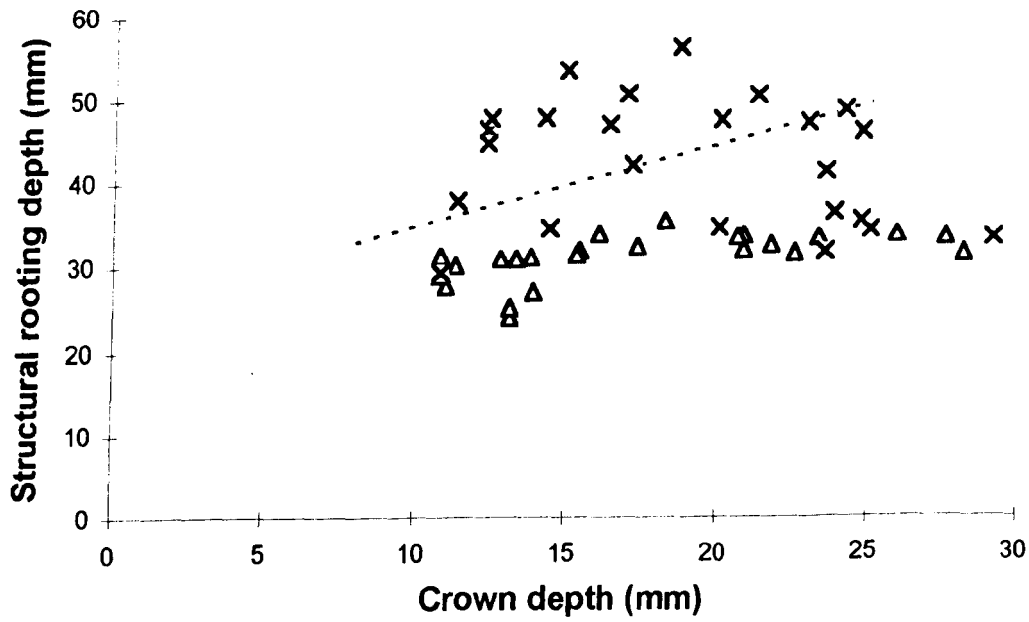

Figure 6.12 Crown depth plotted against structural rooting depth at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The 1:1 relationship (- --) is shown.

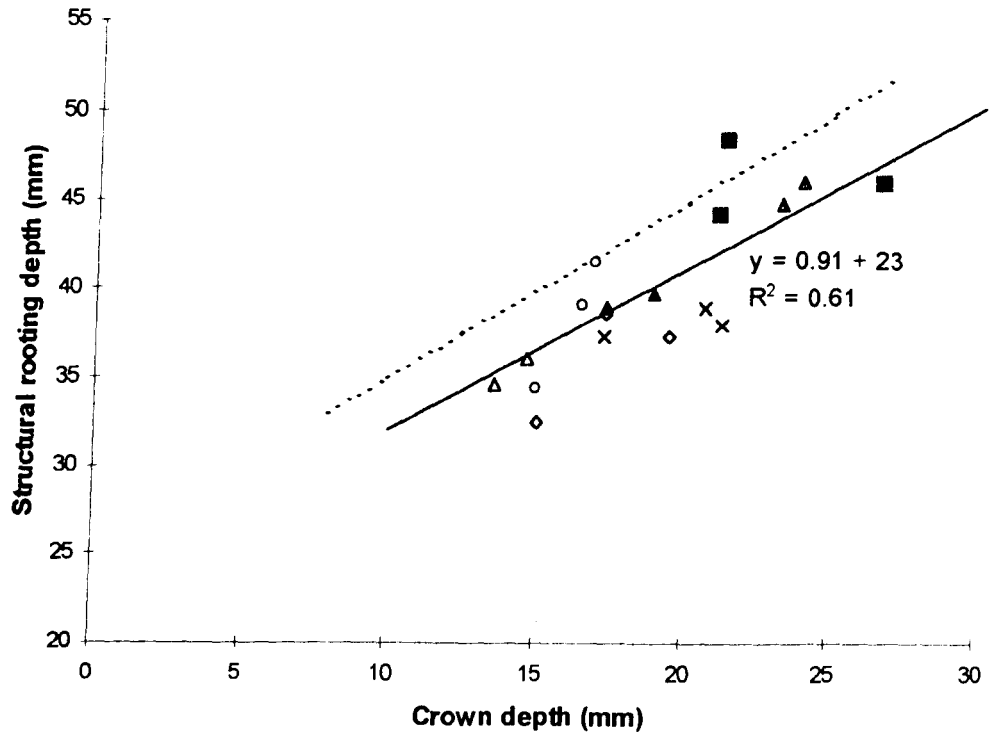

Figure 6.13 Crown depth plotted against structural rooting depth at GS 61 + 75 °Cd for Riband (◇), Hereward (■), Little Joss (×), Beaver (○) and Apollo (▲). The 1:1 relationship (---) and best fit line (—) are shown.

In the husbandry experiments a greater rigid root length was strongly associated with a greater structural rooting depth ($P<0.001$). This effect was strongest in the MT96 experiment in which changes in rigid root length accounted for about 70% variation in the structural rooting depth. The best fit line was also similar to the relationship expected if structural rooting depth was calculated from rigid root length, when a crown depth of 20 mm and an angle of root spread of 90° are assumed. This effect was not found in the VT95 experiment (Figure 6.17).

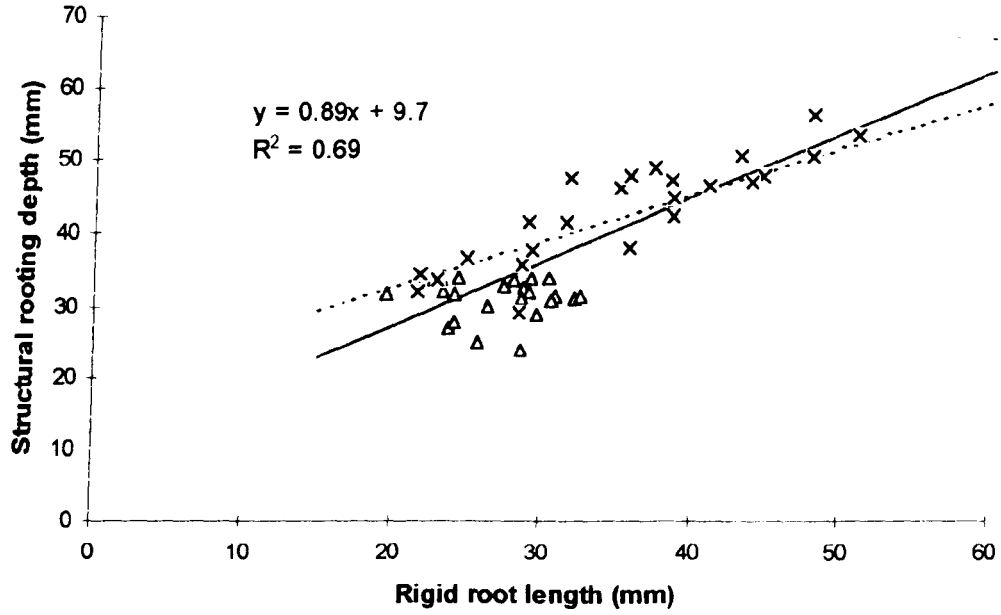

Figure 6.14 Rigid root length plotted against structural rooting depth at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The expected geometrical relationship (---), assuming a root spread of 90° and crown depth of 20 mm, and best fit line (—) are shown.

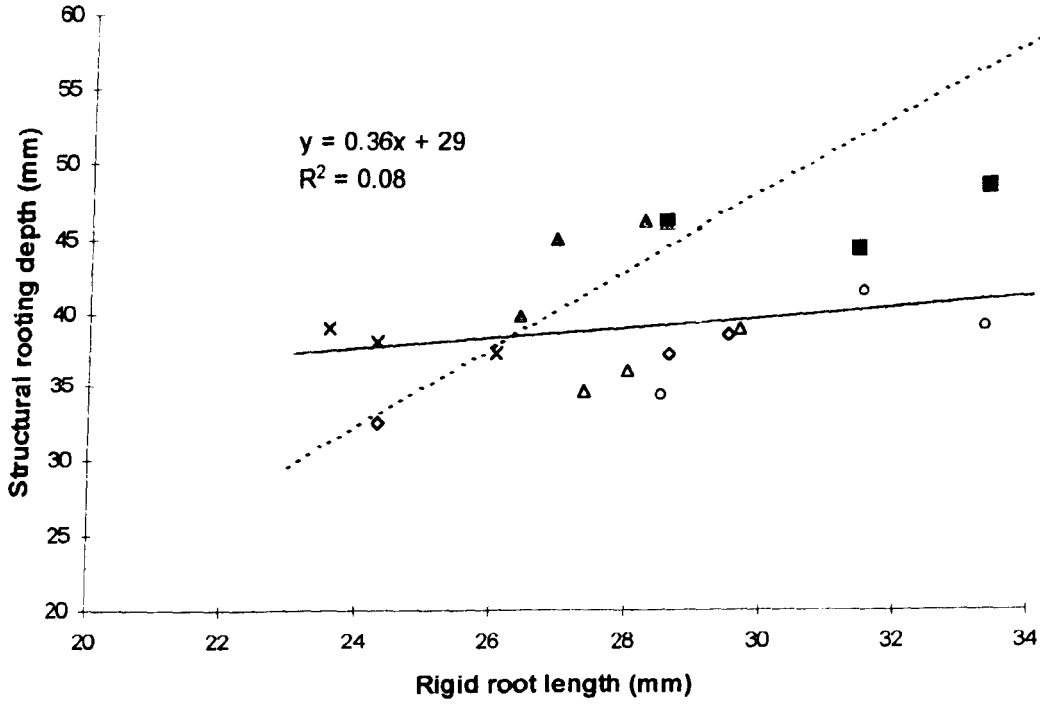

Figure 6.15 Rigid root length plotted against structural rooting depth at GS 61 + 75 °Cd for Riband (◇), Mercia (Δ), Hereward (■), Little Joss (×), Beaver (○) and Apollo (▲). The expected geometrical relationship (---) assuming a root spread of 90° and crown depth of 20 mm and best fit line (—) are shown.

A greater angle of root spread was associated with a smaller structural rooting depth in the MT96 experiment ($P<0.01$; Figure 6.16) and in the VT95 experiment ($P<0.05$; Figure 6.17). The best fit lines were similar to the relationship expected if structural rooting depth was calculated from angle of root spread assuming a rigid root length of 30 mm and a crown depth of 20 mm. Changes in angle of root spread due to husbandry accounted for 59% variation in structural rooting depth in the MT96 experiment, but only 20% variation in the VT95 experiment. A similar relationship was not found in the MT95 experiment.

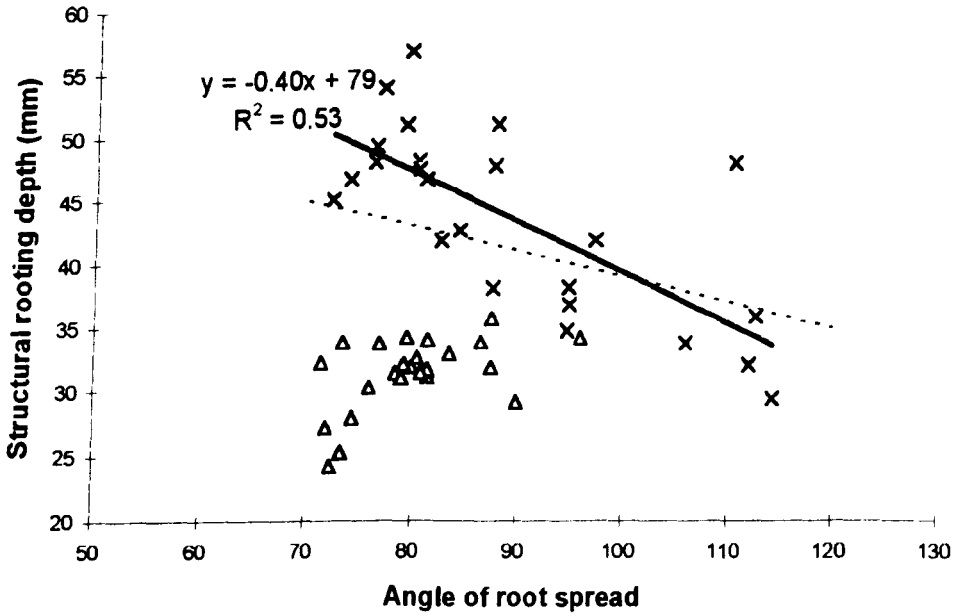

Figure 6.16 Angle of root spread plotted against structural rooting depth at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The expected geometrical relationship (---), assuming a rigid root length of 30 mm and a crown depth of 20 mm , and best fit line (—) are shown.

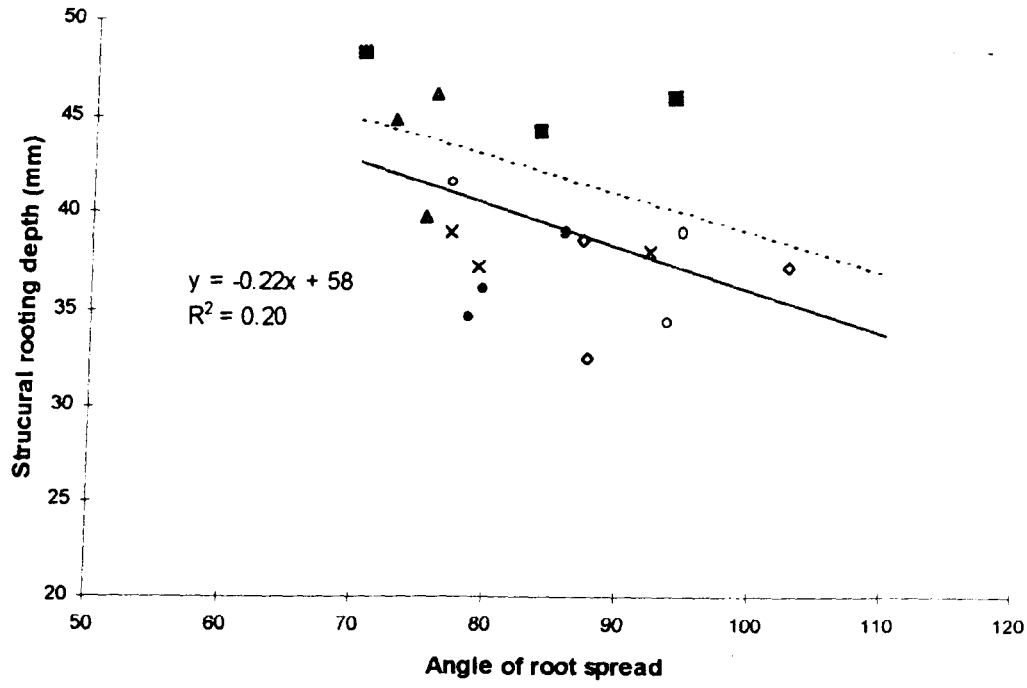

Figure 6.17 Angle of root spread plotted against structural rooting depth at GS 61 + 75 °Cd for Riband (◇), Hereward (■), Little Joss (×), Beaver (○) and Apollo (▲). The expected geometrical relationship (---) assuming a rigid root length of 30 mm and a crown depth of 20 mm and best fit line (—) are shown.

In summary, variation in structural rooting depth due to husbandry was mainly a result of changes in rigid root length and to a lesser extent angle of root plate spread. Differences in plant population density probably caused the differences in rigid root length and structural rooting depth. Genotypic variation in structural rooting depth was mainly due to changes in crown depth and to a lesser extent angle of root spread. Genotype had a small effect on rigid root length in comparison with plant population density.

6.2.2 Predicting structural rooting depth

The experiments have shown that structural rooting depth undergoes only modest changes between GS 30 and GS 69-71, with no distinct developmental trend apparent in MT95 or MT96 experiments. This suggests that spring measurements of structural rooting depth may be used to represent the summer-time values directly. There was a statistically significant relationship between structural rooting depth measured at GS

30 and at GS 69-71 in the MT95 and MT96 experiments ($P<0.05$; Figure 6.18). In addition, the best fit line was very similar to the 1:1 relationship, thus suggesting that spring values of structural rooting depth could represent summer-time values (Equation 6.2).

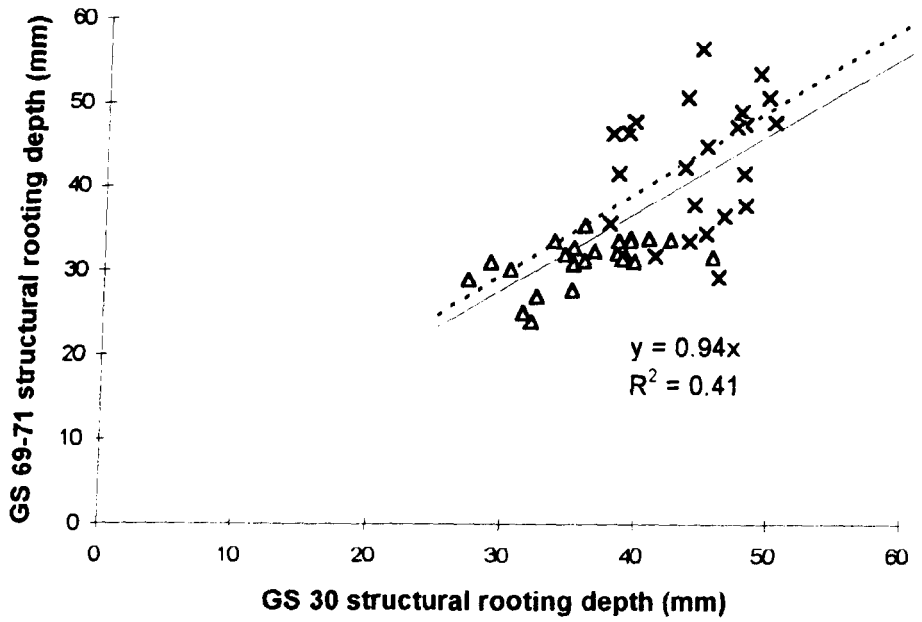

Figure 6.18 Structural rooting depth measured at GS 30 plotted against structural rooting depth at GS 69-73 for the MT95 (Δ) and MT96 (×) husbandry experiments. The 1:1 relationship (---) and best fit line (—) are shown.

$$L_c = L_s \qquad \textbf{(Equation 6.2)}$$

Lc - structural rooting depth (mm) at start of stem extension

Ls - structural rooting depth (mm) in summer

Analysis of Figure 6.18 shows that GS 30 measurements of structural rooting depth mainly accounted for variation between seasons. It appears to account for a small amount of the variation within each season. At this point it should be remembered

that there were no large treatment differences for structural rooting depth. The largest difference at GS 71 was due to seed rate and was only 6 mm. In addition, early season treatment differences were even smaller. In fact, much of the within-season variation was due to natural variation, as structural rooting depth often had a coefficient of variation between plots of 20 %. These findings probably explain why the small treatment differences were not accounted for.

It was shown in Chapter 5 that rigid root length increased between GS 30 and GS 39. This would be expected to cause structural rooting depth to increase over this period. Such an increase was observed in the VT95 experiment, but not in the MT95 or MT96 experiments. Thus, it is uncertain whether structural rooting depth remains constant from GS 30 onwards. If it increases after GS 30 then the prediction scheme in equation 6.2 would become less useful. It would therefore seem prudent to develop an additional prediction scheme which does not assume that structural rooting depth remains constant from GS 30 onwards.

Variation in structural rooting depth due to husbandry was mainly a result of changes in rigid root length. Therefore, a prediction of rigid root length may account for variation in rooting depth. Spring plant number has already been shown to account well for variation in rigid root length. Therefore, spring plant number may be indicative of structural rooting depth, as it was for root plate spread. However, no statistically significant relationship was found between spring plant number and the summer-time structural rooting depth (Figure 6.19), although a trend was apparent for smaller plant populations to be associated with deeper structural roots in the MT96 experiment.

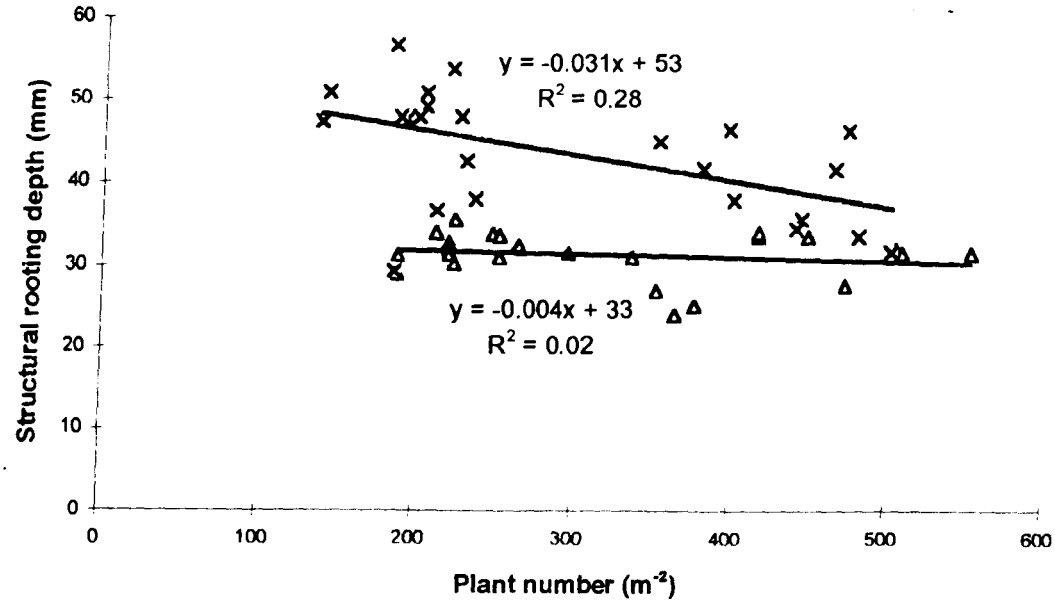

Figure 6.19 Plant population plotted against structural rooting depth at GS 69-71 for the MT95 (Δ) and MT96 (×) husbandry experiments. The best fit lines (—) are shown for the MT95 and MT96 experiments.

6.2.3 Conclusions

The largest differences in structural rooting depth were due to season and genotype. Structural rooting depth measured at GS 30 predicted the seasonal differences reasonably well. This measurement would also be expected to account well for the genotypic differences, whose rankings remained constant between GS 30 and GS 61 (5.4.2). To predict the relatively modest differences in structural rooting depth due to husbandry, it appears that more precise measurements must be made. As with root plate spread, greater numbers of plants may need to be measured to reduce the large amount of variation associated with this character. This prediction assumes that structural rooting depth remains unchanged from GS 30 onwards. This is uncertain and there is evidence to suggest that structural rooting depth increases slightly after GS 30. If this was proven then the prediction scheme should be modified to take this into account.

Plant density did not relate well to structural rooting depth. This was probably because plant density only affected one out of the three influential components of

structural rooting depth. This was unlike root plate spread in which two out of three of its components were strongly influenced. This, in conjunction with the large natural variation of structural rooting depth meant that plant population density exerted an influence which was too small to be used for predicting this plant character.

7. PREDICTING STEM FAILURE MOMENT

In comparison with the structural rooting characters there is more scientific literature concerning stem failure moment and its components; stem diameter, stem wall width and failure yield stress. This has enabled a quantitative prediction scheme to be set up for two of its components, stem diameter and stem wall width. This prediction scheme is based entirely on the literature which allows it to be tested in the lodging experiments. Stem failure yield stress is less well understood and empirical prediction schemes have been suggested and developed in the lodging experiments.

It would be advantageous if a common method would serve to predict all the components of stem failure moment. A study of the literature has suggested that stem dry weight per unit length may fulfil this role. Stem dry weight per unit length is positively correlated with stem failure moment (Atkins, 1938) and reviews on lodging by Mulder (1954) and Pinthus (1973) have stated stem dry weight per unit length to be related to stem diameter and stem wall width. Stem failure yield stress has been related to the thickness of the lignified cell layer of the stem wall (Crook *et al.*, 1993), in particular the vascular and sclerenchyma tissues (Pinthus, 1973). Sachs and Kofranek (1963) showed that conditions which reduced stem diameter and stem wall width caused smaller and fewer cells across the pith, cortical and vascular regions of the stem. This suggests that indicators of failure yield stress, the width of the lignified layer of cells, may be correlated with stem diameter and stem wall width. Hence, it is proposed that estimates of stem diameter and wall width can be gained from a prediction of stem dry weight per unit length, and that stem failure yield stress may be related to stem diameter and wall width.

7.1 PREDICTING STEM DIAMETER AND WALL WIDTH

7.1.1 Setting up the prediction scheme

Stem dry weight of the basal internodes of wheat was between 1.2 and 1.5 mg mm^{-1} (Mulder, 1954). It seems reasonable to propose that stem dry weight per unit length

is determined by the balance between the dry matter supply to the stem (source) and the dry matter consumption by the stem (sink) during its formation. The dry matter supply to the whole crop can be estimated crudely from the amount of radiation intercepted by the crop canopy during stem extension by assuming the efficiency with which wheat converts light energy to dry matter as 2.3 g MJ^{-1} PAR (Gallagher and Biscoe, 1978). The total proportion (P) of solar radiation which is not intercepted by the canopy is given by Beer's law (Monsi and Saeki, 1953), see Equation (7.1), which requires values for the canopy size (L) and its extinction coefficient (k).

$$P = e^{-kL} \qquad \textbf{(Equation 7.1)}$$

Canopy size can be observed in the spring, the extinction coefficient can be measured in the spring or estimated as 0.46 (Thorne *et al.*, 1988) and the incident radiation can be estimated from long term weather records or observed. The proportion of dry matter which is partitioned to the stems during early stem extension may be assumed to be 40 % (Weir *et al.*, 1984; Foulkes *et al.*, 1993). Finally, the dry matter which is partitioned to each individual stem is calculated by dividing the total dry matter partitioned to all the stems in a crop by the number of extending stems observed at the beginning of stem extension.

If April is taken as the period when most crops undergo early stem extension then using long term weather records at Rosemaund (1959 to 1996) an average daily temperature of 7.8 °C and an average daily PAR of 12.6 MJ m^{-2} may be assumed. To give an example of the type of figures this scheme gives - it is estimated that each stem of a crop with a small canopy of GAI one, which typically had 500 shoots m^{-2} at GS 31, will accumulate 8.5 mg of dry matter per day. For a crop with a large canopy of GAI three and 1500 shoots m^{-2}, it is estimated that each stem will accumulate 5.8 mg of dry matter per day. To standardise calculation methods rates of crop development will be measured in thermal time units (°Cd). Therefore, the crop with

the small canopy will accumulate dry matter at a rate of 1.1 mg $^{\circ}Cd^{-1}$ per stem, and the crop with the large canopy at a rate of 0.7 mg $^{\circ}Cd^{-1}$ per stem.

Dry matter consumption per stem depends upon the rate of stem extension. Stem extension rate can be estimated from the canopy size via a number of intermediary steps, as summarised in Figure 7.1.

A linear relationship exists between wheat canopy size and the light quality (measured as the R/FR ratio) within the canopy, such that the logarithm of the R/FR ratio decreases with increasing canopy size (Holmes and Smith, 1977; Equation 7.2).

$$\log R/FR = -0.223L + 0.148 \qquad \textbf{(Equation 7.2)}$$

The extending internode perceives changes in the R/FR ratio through its phytochrome system (Child and Smith, 1987; Casal and Smith, 1988). The conversion of the R/FR ratio to the phytochrome photo-equilibrium $P_{FR}:P_{TOTAL}$ has been shown to approximate a rectangular hyperbola (Holmes and Smith, 1977) to which the following equation has been fitted (Hayward, 1984; Equation 7.3).

$$P_{FR}:P_{TOTAL} = \frac{0.75}{\left[1+\left(0.35/R/FR\right)\right]} \qquad \textbf{(Equation 7.3)}$$

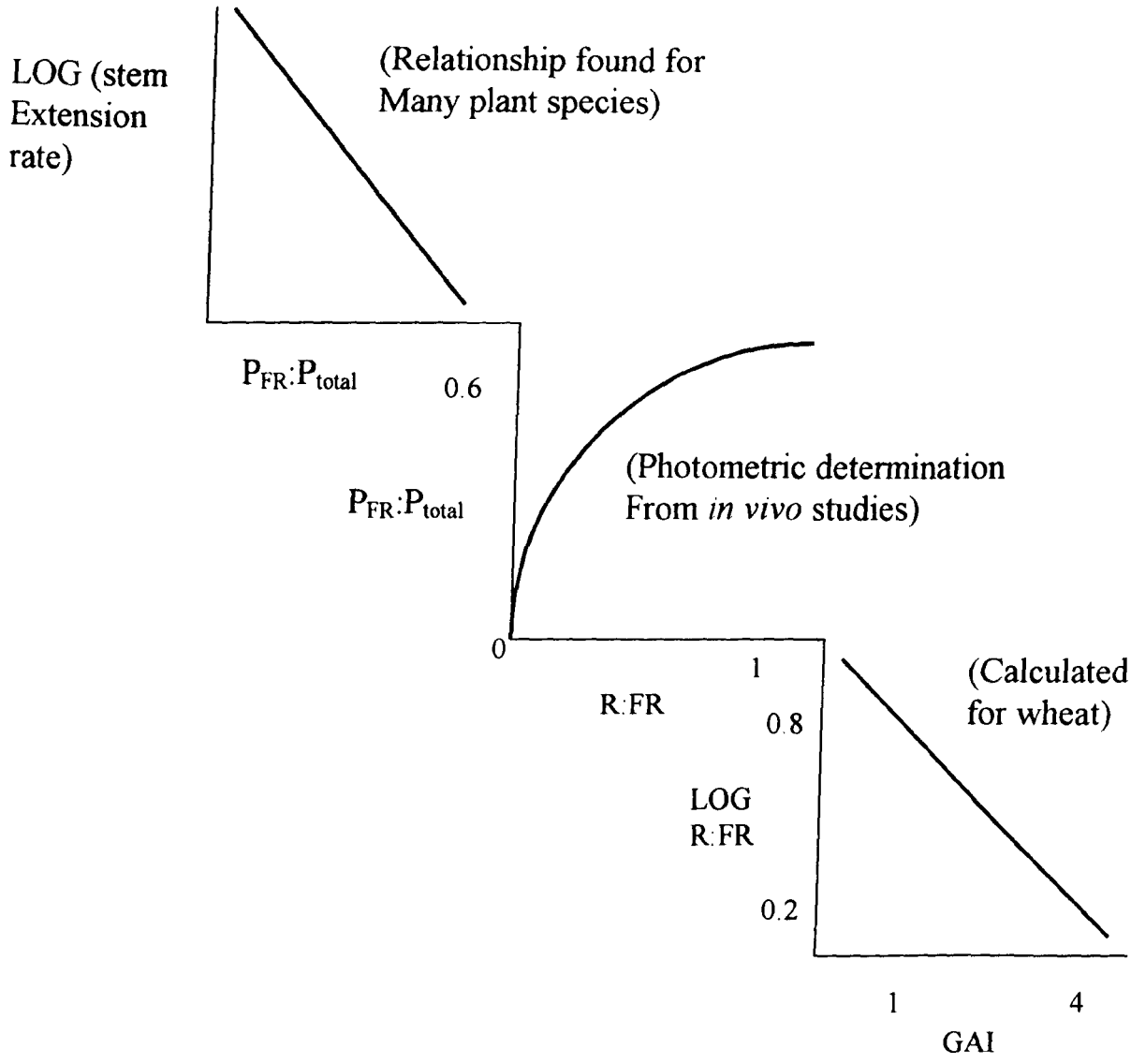

Figure 7.1 Step diagram for the calculation of stem extension rate from green area index.

The phytochrome photo-equilibrium $P_{FR}:P_{TOTAL}$ is linearly related to the logarithm of stem extension rate in a number of arable plant species (Morgan and Smith, 1979). This relationship has a slope which varies from -0.21 for *Senecio vulgaris* to -0.13 for *Sinapis alba*. No such relationship has been reported in the literature for wheat or even any monocotyledonous plant. However, true stem extension rate of wheat is strongly influenced by the R/FR ratio (Casal, 1993) and a linear relationship exists between the rate of leaf-sheath extension in grass species such as *Sporobulus indicus* and the phytochrome photo-equilibrium $P_{FR}:P_{TOTAL}$ (Casal *et al.*, 1987). Thus, there is good evidence that stem extension rate of wheat must be related to canopy size, but the exact relationship is difficult to quantify due to a lack of information about the phytochrome photo-equilibrium $P_{FR}:P_{TOTAL}$ and true stem extension rate. Initially it is proposed to substitute the relationship found for one of the arable weeds tested by Morgan and Smith (1979). *Chenopodium album* was chosen because it showed a 'middle of the range' slope (Equation 7.4) (For more details see section 2.2.1).

$$\log E = -0.083(P_{FR} : P_{TOTAL}) + 0.072 \qquad \textbf{(Equation 7.4)}$$

In summary, stem extension rate (E) can be estimated directly from GAI (L) by combining Equations 7.2, 7.3 and 7.4 , see Equation 7.5.

$$E = 10^{-0.083\left[\frac{0.75}{\left(1+0.35/10^{(0.223L+0.148)}\right)}\right]+0.072} \qquad \textbf{(Equation 7.5)}$$

Equation 7.5 estimates that a crop with a small canopy size of GAI one will have a stem extension rate of 0.62 mm $^{\circ}Cd^{-1}$, and a crop with a larger canopy size of GAI three will have a more rapid stem extension rate of 0.68 mm $^{\circ}Cd^{-1}$.

Stem dry weight per unit length (mg mm^{-1}) can be estimated by dividing the rate at which individual stems accumulate dry matter (mg $^{\circ}Cd^{-1}$) by the rate at which they extend (mm $^{\circ}Cd^{-1}$). Stem dry weights per unit length of 1.8 mg mm^{-1} and 1.1 mg mm^{-1} are calculated for crops with canopy sizes of GAI one and three respectively. These estimates compare with results of Bush and Evans (1988) who found stem dry weight to vary between 0.7 and 1.3 mg mm^{-1} in Australian wheats.

In summary, stem dry weight per unit length is closely related to the lodging-associated plant characters used to calculate stem failure moment. It is most strongly related to stem diameter and stem wall width. A framework for calculating stem dry weight per unit length has been outlined based on the stem dry matter supply and stem dry matter consumption. This requires information about the incident radiation, canopy size and shoot number per unit area at the time that the lower internodes are extending. Once dry weight per unit length has been calculated it can then be used to estimate stem diameter, stem wall width and stem failure yield stress.

Stem dry weight per unit length can be combined with the density (D) of the stem material to calculate the cross sectional area of the stem wall (Equation 7.6). The density of the stem material of the second most basal internode has been calculated as 0.38 mg mm^{-3} and 0.27 mg mm^{-3} for wheat crops with nil and 150 kg ha^{-1} N respectively (Mulder, 1954). Therefore, the cross sectional area may be estimated by dividing the predicted stem dry weight by one of these values of the stem wall density. The stem density calculated from the crop with 150 kg ha^{-1} N will be used because this type of nitrogen application is more widely used by growers than nil nitrogen.

Stem dry weight per unit length $= \pi Dw(d - w)$ **(Equation 7.6)**

To calculate stem diameter (d) and stem wall width (w) from cross sectional area additional information is required about these two unknowns. It can be inferred from work by Sachs and Kofranek (1963) that stem diameter and stem wall width are positively related. This relationship was not quantified. Therefore experimental data has been used to find this relationship (Figure 7.2). Stem diameter and wall width were significantly linked ($P<0.001$), and the exact relationship is given in Equation 7.7. This will be used to estimate values for stem diameter and stem wall width from the predicted cross sectional area of the stem wall.

$$w = 0.25d - 0.18 \qquad \textbf{(Equation 7.7)}$$

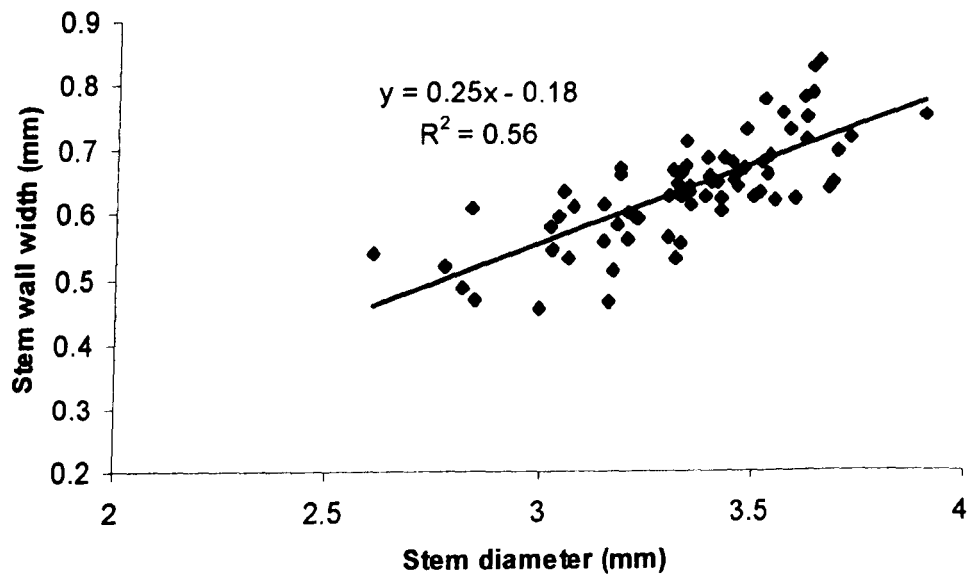

Figure 7.2 Stem diameter plotted against stem wall width at GS 73 in the MT96 experiment.

7.1.2 Testing the prediction of stem diameter and wall width

Stem dry weight per unit length and the stem wall cross sectional area may be predicted for the lower internodes from the shoot number per metre squared and green area index observed at GS 30, together with the average PAR between GS 30 and GS 33 using the methods described in section 7.1.1. The stem wall cross sectional area of internode one has been calculated from the stem diameter and wall width observed at GS 73, and compared with predicted values of stem wall cross sectional area (Figure 7.3). Predicted values were of similar magnitude to the observed values, but this method did not account for variation observed.

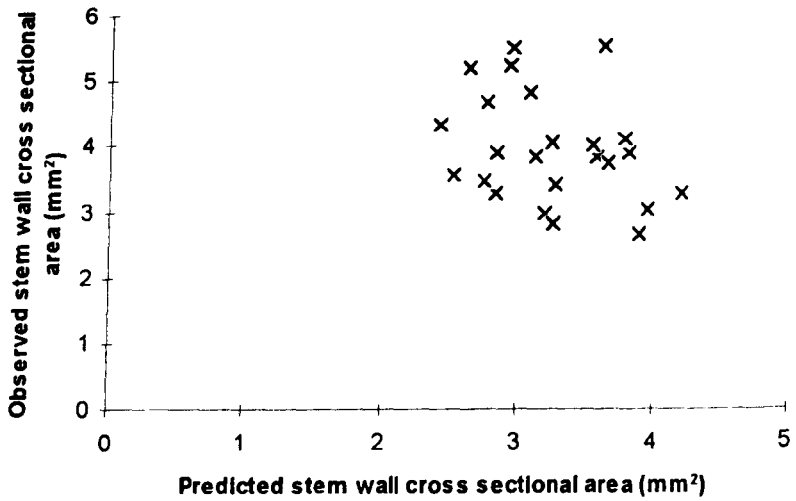

Figure 7.3 Stem wall cross sectional area predicted at GS 30 plotted against stem wall cross sectional area observed at GS 73 in the MT96 experiment.

Internode one extends between GS 30 and GS 33. Therefore the mean values of the crop features during this period will be more representative of the conditions experienced by the extending internode. Consequently a more precise prediction of cross sectional area was gained by taking the mean of the green area index and shoot number per metre squared from samples at GS 30, GS 31 and GS 33 (Figure 7.4). With these more precise estimates, the best fit line accounted for 61 % of the variation

and almost showed a 1:1 relationship, with predicted cross sectional areas being slightly larger than the observed.

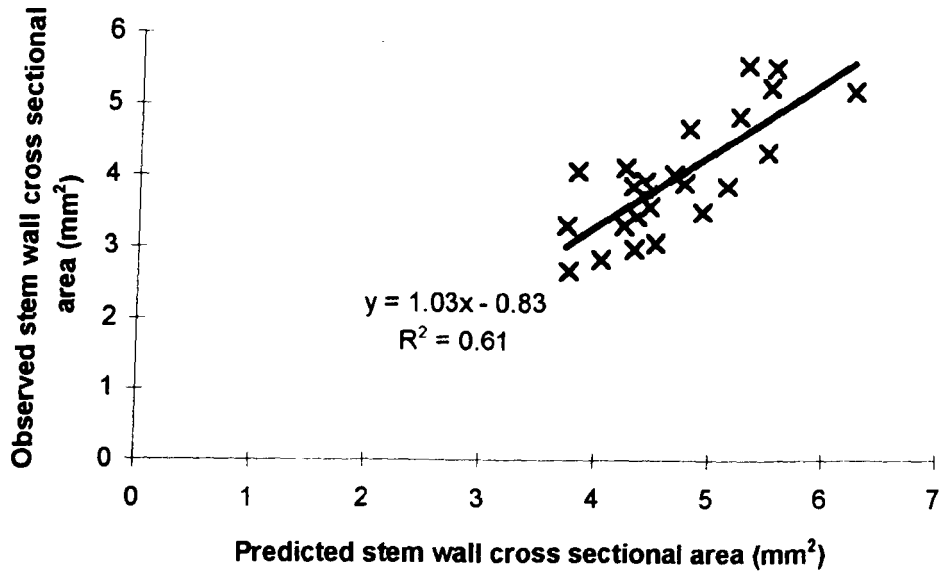

Figure 7.4 Stem wall cross sectional area predicted using mean crop observations between GS 30 and GS 33 plotted against stem wall cross sectional area, calculated from stem diameter and wall width observed at GS 73 in the MT96 experiment.

Predicted and observed stem diameters and wall widths are compared in Figure 7.5 and Figure 7.6. It is acknowledged that this is not a true test for the prediction of stem diameter and wall width because Equation 7.7, used to estimate these characters from the predicted cross sectional area, has been derived from the experiments. The relationships between the observed and predicted parameters are similar to cross sectional area (Figure 7.4), with the predicted stem diameter and wall width slightly greater than the observed.

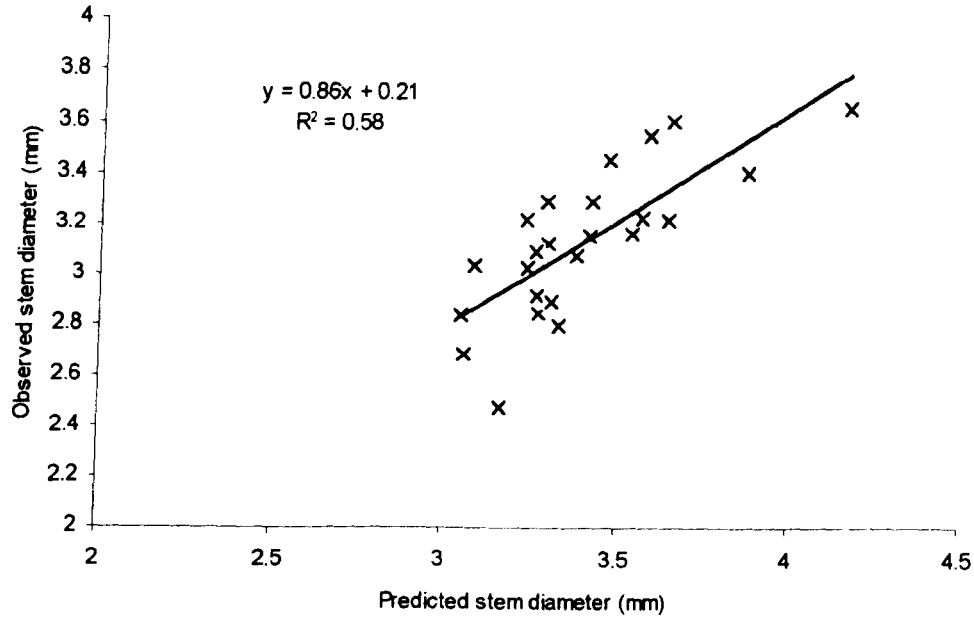

Figure 7.5 Predicted stem diameter against stem diameter observed at GS 73 in the MT96 experiment.

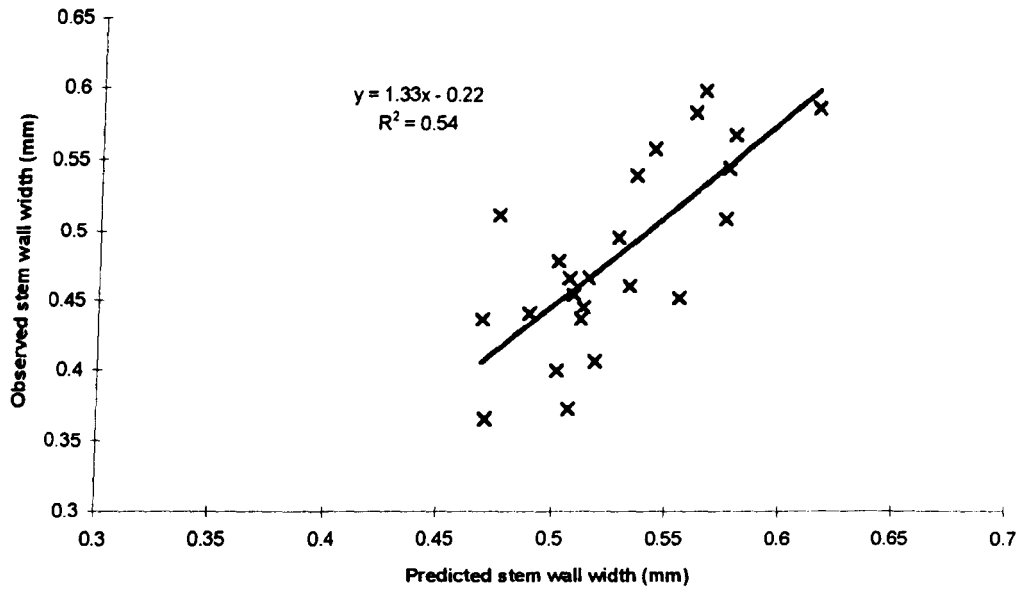

Figure 7.6 Predicted stem wall width against stem wall width observed at GS 73 in the MT96 experiment.

7.1.3 Conclusions

The first attempt at predicting stem diameter and wall width has demonstrated reasonable success. However further improvement is required. One of the main sources of inaccuracy comes from the measurement of shoot number. Predictions of stem diameter and wall width from measurements of green area index and shoot number at GS 30 did not account for the variation observed. This was apparently due to imprecise shoot number counts at a time when shoot numbers were declining rapidly. The variation of the shoot number and green area measurements was reduced by averaging measurements taken during early stem extension at GS 30, 31 and 33. However, in practice the grower requires an estimate of future stem characters and lodging risk at GS 30. Assessing shoot number at this time will always be difficult; although larger sample sizes will improve the estimates.

Many assumptions were made within the calculation including: extinction coefficient, the efficiency which wheat converts light energy to dry matter, the proportion of dry matter which is partitioned to the stem, the density of the stem material and the relationship between the ratio of P_{TOTAL}:P_{FR} and stem extension rate. Improving the accuracy of any one of these should improve the prediction of stem characters. The relationship between the ratio of P_{TOTAL}:P_{FR} and stem extension rate and the density of the stem material are least known and could be the greatest source of error. Both these assumptions can be improved by simple experiments, some of which have been carried out in the Lodging Project.

The relationship between canopy size and stem extension rate in wheat (summarised in Figure 7.1) can be investigated further. The observed rate of leaf-sheath extension between GS 30 and GS 33 has been plotted against the predicted stem extension rate (estimated from green area index using Equations 7.2, 7.3 and 7.4) in Figure 7.7. The observed and predicted values are strongly related, but the predicted values cover a much smaller range than the observed values. It must be noted that leaf-sheath extension is not true stem extension. The rate of true stem extension is difficult to

observe because the extending apex is hidden beneath leaf-sheaths. However, it is hoped that the rate of leaf-sheath extension will give an indication of the rate of true stem extension and it will certainly give an indication of the rate at which dry matter is utilised by the stem. The experimental results in Figure 7.7 suggest that the magnitude by which the rate of stem extension changes in response to canopy size has been under-estimated in the prediction scheme. This means that the variation in the amount of dry weight accumulated in stems extending within different sized canopies may have been under-estimated.

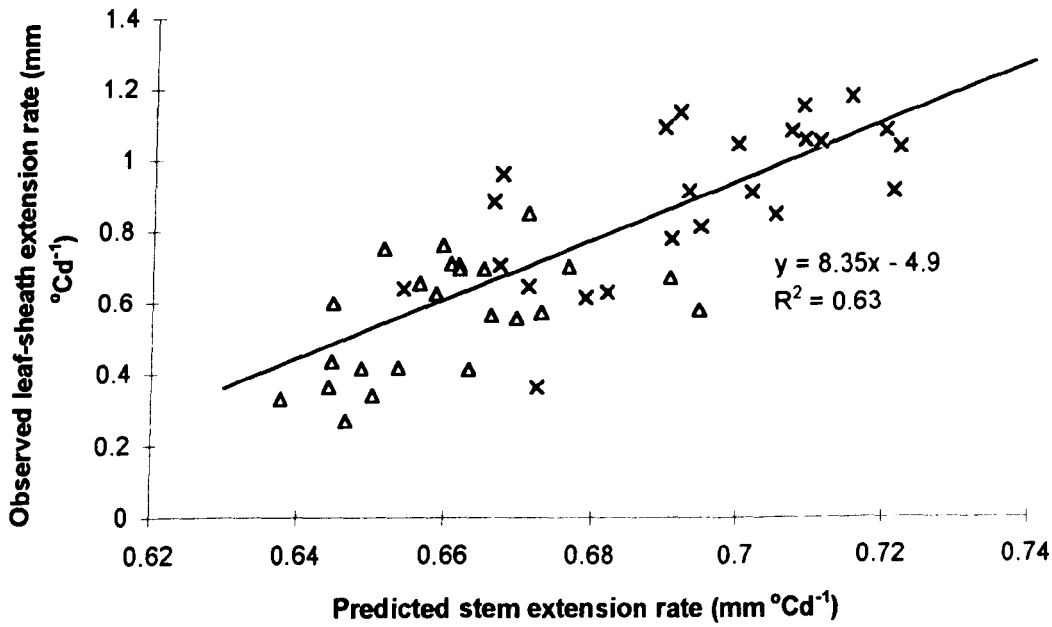

Figure 7.7 Predicted stem extension rate plotted against observed leaf-sheath extension rate between GS 30 and GS 33 for the MT95 (□) and MT96 (□) husbandry experiments.

Why this possible discrepancy has arisen will now be investigated. Three relationships (Equations 7.2, 7.3 and 7.4) have been used to predict stem extension rate from canopy size. The first two equations should be reasonably robust as the first is derived from wheat and the second is applicable to all plant species. However the third, which quantifies the relationship between stem extension rate and the phytochrome photo-equilibrium, was derived from *Chenopodium album*. It is likely that this relationship will be different for wheat. Experiments of Casal (1993) and those reported here suggest that wheat is considerably more sensitive to changes in

the phytochrome photo-equilibrium. Further experiments in this area will be needed to quantify this relationship and improve the accuracy of this part of the prediction.

7.2 PREDICTING STEM FAILURE YIELD STRESS

It has been proposed that stem failure yield stress is related to the thickness of the lignified layer within the stem wall (Pinthus, 1973; Crook *et al.*, 1993), which in turn is related to stem diameter and wall width (Sachs and Kofranek, 1963). This idea has been investigated in the lodging experiments by comparing observed values for failure yield stress with stem wall width (Figure 7.8), stem diameter (Figure 7.9) and stem wall cross sectional area (Figure 7.10).

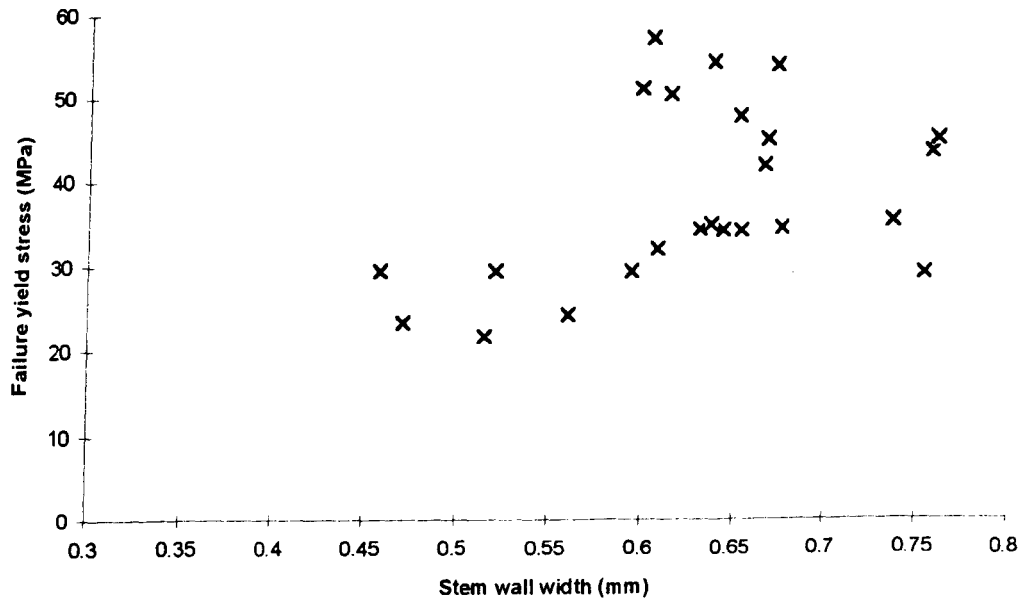

Figure 7.8 Stem wall cross sectional area plotted against stem failure stress observed at GS 73 in the MT96 experiment.

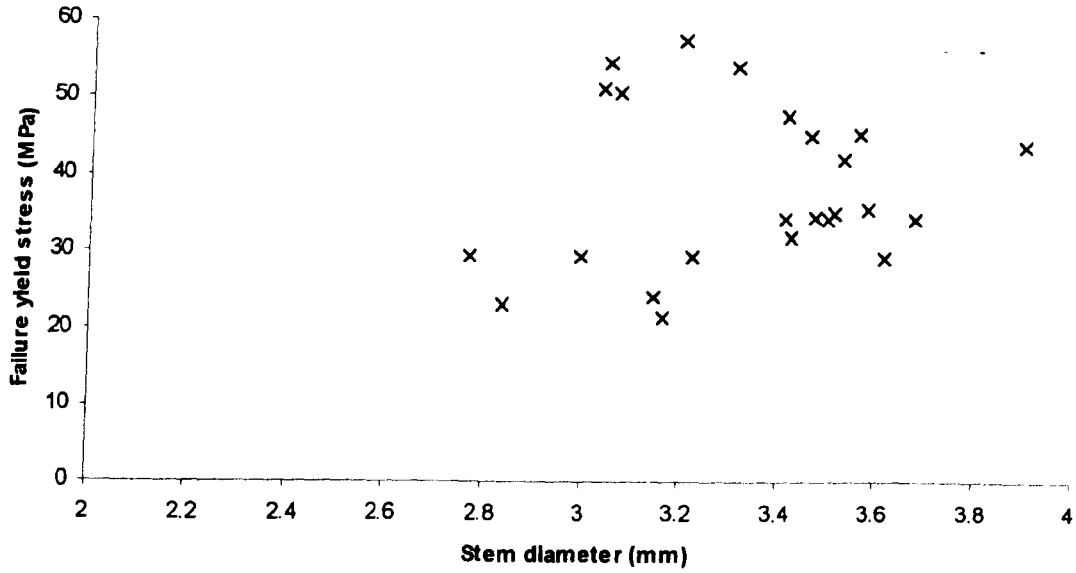

Figure 7.9 Stem diameter plotted against stem failure stress observed at GS 73 in the MT96 experiment.

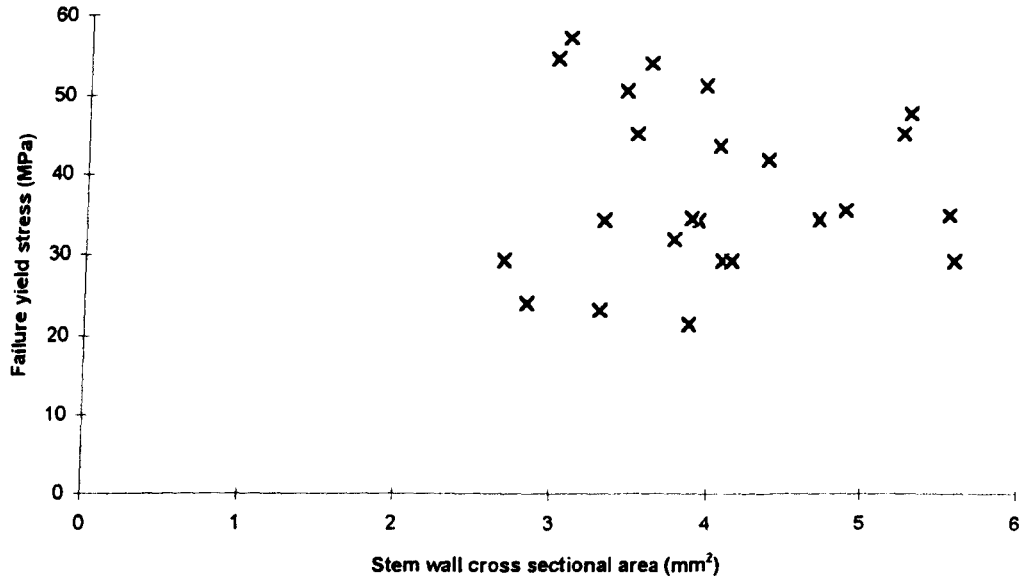

Figure 7.10 Stem wall cross sectional area plotted against stem failure stress observed at GS 73 in the MT96 experiment.

Failure yield stress behaved independently of stem wall width, stem diameter and stem wall cross sectional area. This could mean that the thickness of the lignified layer is not related to the width of the stem wall, as originally inferred from Sachs and Kofranek (1963). Alternatively, stem failure yield stress may not be related to the

thickness of the lignified layer, as was suggested by Pinthus (1973) and Crook *et al.*, (1993). It may be that the arrangement and interaction of the structural carbohydrates and lignin in the stem cell walls are more important in stem failure yield stress than the concentrations of these components (Knapp *et al.*, 1987). A microscopic investigation would be required to elucidate how failure yield stress is determined; this is beyond the scope of the present study. However, the lodging experiments have determined agronomic factors that influence failure yield stress, and these may prove useful for understanding this stem character.

High residual nitrogen in combination with early sowing caused a statistically significant reduction in stem failure yield stress, although this effect was inconsistent. These results suggest that stem failure yield stress is related to the etiolation effects associated with large early season canopies, brought about by high nitrogen levels. However, this was found not to be the case earlier in this section, when comparisons were made between failure yield stress and stem diameter, and another explanation must be sought. Mulder (1954) suggested that high nitrogen concentrations reduced failure yield stress by reducing the thickness of sclerenchyma cell walls and their lignin content. More thorough investigations would be needed to confirm this. However, it suggests that a prediction of failure yield stress may be developed from the quantity of nitrogen supplied to the crop, particularly the soil residual nitrogen supply.

In conclusion, this important component of stem failure moment is difficult to predict because there is uncertainty as to which factors affect it and by what mechanisms. This study has shown that stem failure yield stress behaves independently of the geometric properties of the stem and is quite variable. Genotype also had a large influence on failure yield stress. High levels of soil residual nitrogen reduced failure yield stress, but effects were inconsistent. Future investigations should concentrate on these areas for developing a prediction of this plant character. It should also be noted that values of stem failure yield stress remained reasonably constant from GS 39 until harvest. This will be useful in supporting decisions about the application of late PGRs.

8. PREDICTING BASE BENDING MOMENT

Natural frequency and height at height at centre of gravity are used to calculate shoot base bending moment, which is then multiplied by shoot number per plant to calculate plant base bending moment. The most valuable prediction scheme was for shoot number per plant (Table 5.21) with natural frequency and height at centre of gravity having less importance. Accordingly a relatively thorough prediction scheme has been developed for final shoot number per plant. Prediction schemes have not been developed for natural frequency or height at centre of gravity. However, the complex relationship between these two characters has been elucidated and their component parts identified and ranked in order of their influence on the main character, thus paving the way for future research to develop prediction schemes for these plant characters.

8.1 FINAL SHOOT NUMBER PER PLANT

8.1.1 Setting up the prediction scheme

Final shoot number per plant is calculated from the final shoot number per metre squared divided by the plant number per metre squared. Plant number per metre squared can be measured at or before GS 30 and seldom changes from spring onwards. Final shoot number per metre squared is influenced by many factors including plant number per metre squared. Reducing seed number (which usually approximates to plant number) from 400 seeds m^{-2} to 100 seeds m^{-2} caused a reduction in final shoot number from 582 to 430 shoots m^{-2} (Darwinkel, 1978). This showed that final shoot number per metre squared underwent significant, but relatively small changes in response to large variation in plant number per metre squared. A 75 % reduction in seed number only reduced final shoot number by 26 %. This effect is due to the wheat plant's ability to compensate for low plant populations by producing and maintaining more tillers. It can be estimated that the reduction in seed number per metre squared (cited above) was associated with an increase in shoot number per plant from 1.5 to 4.3. Given these findings, plant number per metre

squared alone is expected to bear a strong negative relationship with final shoot number per plant.

Unlike plant number per metre squared, shoot number per metre squared has a very variable pattern of development. Wheat crops begin tillering soon after their third leaf has emerged and this continues until around the double ridges stage. At this point the maximum shoot number per metre squared is reached and the most recently formed tillers begin to die. The proportion of the maximum shoot number which survives is governed by the competition for resources between shoots. This will mean that for a given level of resources, the proportion of shoots surviving will be inversely related to the maximum shoot number per metre squared. The level of resources depend upon the supplies of nitrogen, radiation and water, with varieties responding differently to these limiting factors. Tiller death continues until around anthesis when the final shoot number per metre squared stabilises. A method is required which takes into account this pattern of tiller death and its influencing factors and predicts final shoot number per metre squared at GS 30.

The maximum potential final shoot number per metre squared is set by the maximum shoot number achieved in spring. Simons (1982) has shown that the final shoot number per metre squared is often related to the maximum shoot number. An estimate of the maximum shoot number can be gained by measuring shoot number per metre squared at GS 30.

A model for shoot survival has been adapted from Porter *et al.* (1984). This can be used at the time of maximum shoot number to estimate the probability of individual tillers surviving until anthesis (Equation 8.1). This equation is based upon that described by Landsberg (1977) and used by Landsberg and Thorpe (1975) in a model of apple bud morphogenesis. To calculate the probability of each tiller surviving it is assumed that all main shoots survive, that the rate of tiller death is a function of shoot density, that the last formed tillers die first and that tiller death occurs between double ridges and anthesis. Therefore, the likelihood of a tiller surviving is determined by the

number of shoots m^{-2} present when it emerged and the expected photothermal duration of the tiller death phase. For example, the first formed tiller in a plant population of 250 plants m^{-2} has a 95 % chance of surviving until anthesis, and the one thousandth formed tiller has only a 10 % chance of survival. By starting with the plant number per metre squared (as a substitute for main shoot number), the maximum shoot number (as observed at GS 30) and the expected photothermal duration of the tiller death phase this method can be used to calculate the probability of each individual tiller surviving until anthesis. From this, the final shoot number per metre squared can be calculated. This model has been calibrated empirically by Porter *et al.* (1984) to give the constants A, a and b, using data from experiments involving the winter wheat variety 'Hustler' grown at an early and late sowing date over three seasons (Weir *et al.*, 1984). These crops were described as having adequate nutrients and water.

$$P = \frac{1}{1 + \left(\frac{T_t / 400}{(A / N_n)^a} \right)^b} \qquad \textbf{(Equation 8.1)}$$

(adapted from Porter *et al.*, 1984)

P - probability of a tiller surviving

T_t - photo thermal time between double ridges and anthesis

N_n - number of shoots per metre squared when each new tiller emerged

A - 825

a - 1.46

b - 2.24

The proportion of tillers surviving is dependent upon the competition for resources by the tillers. The level of this competition will depend upon the balance of resource supply and demand. This model of tiller survival accounts for much of the variation in resource demand by taking account of shoot number per metre squared. However, it

does not take into account variation in resource supply, in terms of nitrogen, radiation and water supplies. It is acknowledged that these factors, particularly nitrogen and radiation, have a strong influence on the proportion of the maximum shoot number surviving. However, due to the lack of quantitative information in the literature about the effect of these factors on shoot number, it is expected that further work will be required with specifically designed experiments to incorporate these factors into the tiller survival model. Another potential source of error arises from the calibration of the model using the variety Hustler. It is likely that Mercia will have a different pattern of tiller death to Hustler and would cause the photo thermal duration between double ridges and anthesis and constants A, a and b to be different. It is expected that further work on different varieties will be required to incorporate the effect of genotype on final shoot number into this model.

In summary, it has been shown that final shoot number per plant can be calculated by dividing the final shoot number per metre squared by the plant number per metre squared. Plant number per metre squared can be counted in the spring. More accurate plant counts can be made in the autumn before tillering, but over winter plant losses may affect this estimate. A prediction of final shoot number per metre squared based on a model of tiller survival has been adapted from Porter *et al.* (1984). This takes into account some, but not all of the influential factors, and its limitations are acknowledged. However, it is hoped to be sufficient for providing a first attempt at predicting shoot number per plant from spring measurements.

8.1.2 Testing the prediction scheme

The first step predicts final shoot number m^{-2} (ear number m^{-2}) using the tiller death model of Porter *et al.* (1984) (Equation 8.1). The second step calculates the final shoot number per plant by dividing predicted final shoot number per metre squared by the observed spring plant number per metre squared.

Equation 8.1 was used to predict ear number m^{-2} in the MT95 and MT96 lodging experiments, using plant and shoot numbers observed at GS 30 together with a

photothermal tiller death duration of 600 °C d^{-1} (Weir *et al.*, 1984). A comparison of predicted final shoot (ear) number m^{-2} with observed ear number m^{-2} is shown in Figure 8.1. This shows that the high ear numbers in the MT96 experiment were correctly predicted and 52 % of the variation was accounted for by the best fit line which was very similar to a 1:1 relationship. This method accounted for the large differences between seasons, but accounted less well for the differences within seasons. It appears that the low maximum shoot number in the MT95 experiment was influential in causing a low ear number in this season. It is likely that modifying the model to account for nitrogen supply will help account for variation in ear number within the seasons.

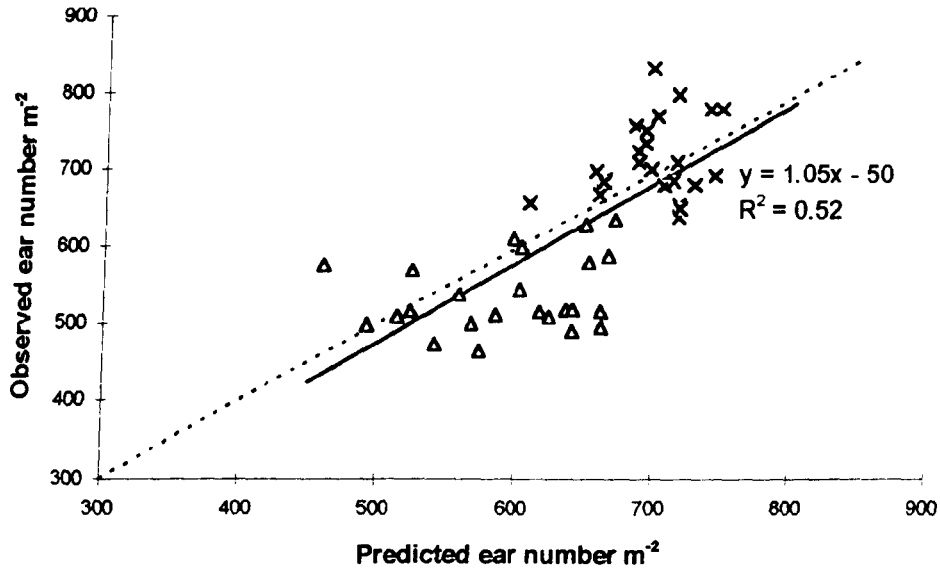

Figure 8.1 Predicted ear number m^{-2} plotted against observed ear number m^{-2} for the MT95 (Δ) and MT96 (×) husbandry experiments. The ideal 1:1 relationship (---) and best fit line (—) are given.

The second step is the calculation of ear number per plant by dividing the predicted ear number m^{-2} by the plant population m^{-2} which was measured at GS 30. Figure 8.2 shows a comparison of the predicted and observed ear number per plant for the MT95 and MT96 lodging experiments. A very strong relationship was found in which 94 % of the variation was accounted for by the best fit line which was very similar to a 1:1 relationship. The large increase in the amount of variation accounted

for between the prediction of ear number per metre squared and final ear number per plant demonstrates the large influence which plant number has on final ear number per plant. These results illustrate the ability of wheat crops to compensate for low plant populations by producing and maintaining more tillers. It is this property which makes plant population such an important predictor of final ear number per plant. This also suggests that an accurate estimation of final shoot number per metre squared is not critical in this prediction scheme.

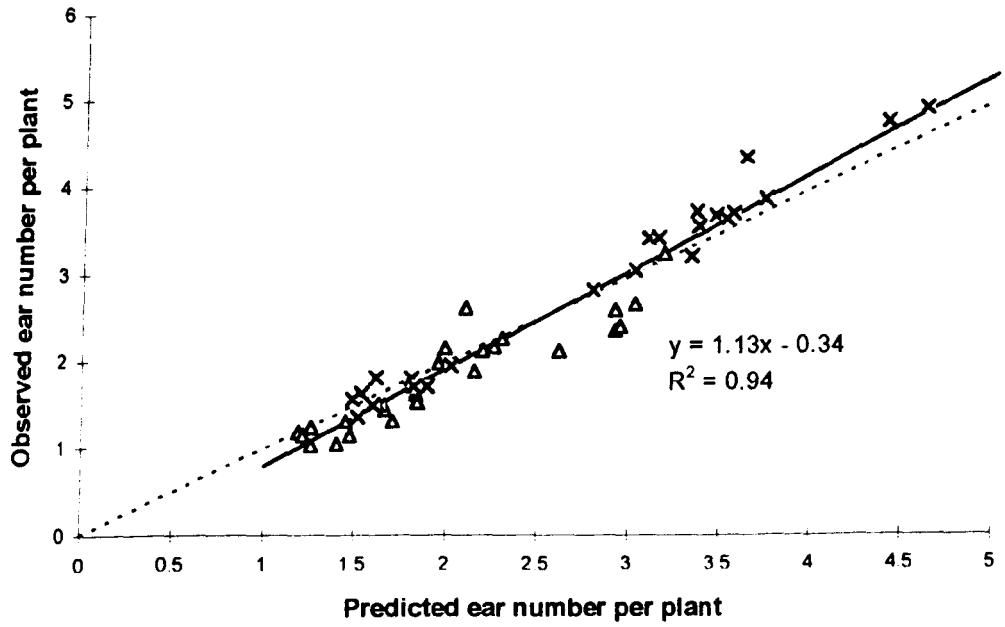

Figure 8.2 Predicted ear number per plant plotted against observed ear number per plant for the MT95 (Δ) and MT96 (×) husbandry experiments. The ideal 1:1 relationship (---) and best fit line (—) are given.

8.2 NATURAL FREQUENCY AND HEIGHT AT CENTRE OF GRAVITY

In this section an empirical relationship is developed which enables natural frequency to be calculated from height at centre of gravity. In addition the components of height at centre of gravity are identified and their relative importance discussed.

8.2.1 Natural frequency

Under dry soil conditions Baker (1995) gives a relationship for natural frequency as a function of height at centre of gravity, ear weight, root ball resistance and stem stiffness. These components of natural frequency could be predicted by secondary prediction schemes and used to estimate natural frequency. However, their relationship with natural frequency is based on the assumption that the crop can be represented by a mass on top of a weightless elastic stem. Baker (1997, personal communication) suggests that it would be unwise to use this essentially idealised equation in a predictive sense, and it would be more sensible to simply regard it as indicating a functional relationship between natural frequency and height at centre of gravity, ear weight, root ball resistance and stem stiffness. It can be inferred from the relationship that a greater height at centre of gravity and ear weight will decrease natural frequency, which will increase shoot base bending moment. Greater stem stiffness and root ball resistance will increase natural frequency, which will decrease shoot base bending moment. In addition it is clear that height at centre of gravity is the most influential component of natural frequency (Baker, 1995). Therefore, an empirical relationship for natural frequency with height at centre of gravity will be investigated in the experiments.

8.2.1.1 A relationship between natural frequency and height at centre of gravity

A strong negative relationship was found between height at centre of gravity and natural frequency measured at GS 73 in the MT96 experiment (Figure 8.3). A similar relationship was found between height at centre of gravity measured at GS 69 and natural frequency measured at GS 85 in the MT95 experiment (Figure 8.4). Care must be taken when interpreting Figure 8.4 because height at centre of gravity and natural frequency were measured at different stages of plant development, and both

plant characters have been shown in Chapter 5 to change in value between GS 69 and GS 85. Therefore the relationship given in Figure 8.4 should only be used to support other evidence for a negative relationship between height at centre of gravity and natural frequency.

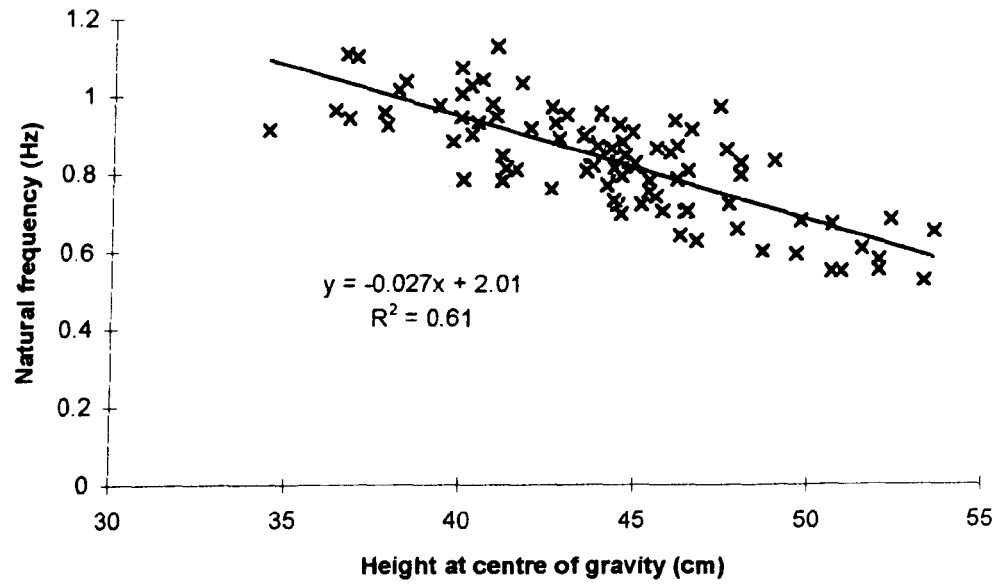

Figure 8.3 Height at centre of gravity plotted against natural frequency at GS 73 for all treatments in the MT96 experiment.

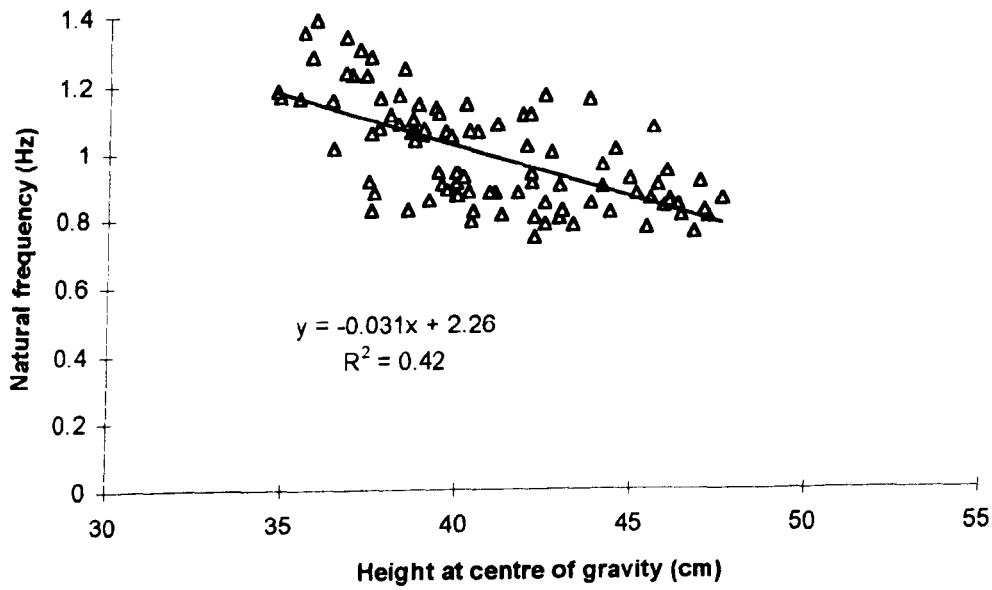

Figure 8.4 Height at centre of gravity at GS 69 plotted against natural frequency at GS 85 for all treatments in the MT95 experiment.

The relationship in Figure 8.3 gives an empirical equation (Equation 8.2) which allows natural frequency to be estimated from the height at centre of gravity.

$$no = -0.027X + 2.01 \qquad \textbf{(Equation 8.2)}$$

no - natural frequency (Hz)

X - height at centre of gravity (cm)

This equation must be tested with data from other varieties and from other growth stages. The latter is particularly important because both natural frequency and height at centre of gravity have different patterns of development during the lodging risk period (Figure 5.11 to Figure 5.14), which suggests that their relationship will change. It is acknowledged that this relationship cannot account for all variation in natural frequency because it does not take into account stem stiffness or root ball resistance. These two factors can influence natural frequency without affecting height at centre of gravity. This was illustrated by the effects of seed rate. Low seed rate increased natural frequency but had little or no effect on height at centre of gravity. This probably happened because low seed rate increased stem stiffness and/or root ball resistance. However, despite using data from different seed rates, Equation 8.2 accounted for a large proportion of the variation. This suggests that stem stiffness and root ball resistance are relatively minor factors influencing natural frequency. Nevertheless, these plant characters should be investigated in future experiments to improve the estimation of natural frequency. In addition, the modifying influences of soil shear strength and canopy wetness on natural frequency must be taken into account when improving Equation 8.2.

8.2.2 Height at centre of gravity

The components of height at centre of gravity are stem height, stem fresh weight, leaf fresh weight, ear fresh weight and ear length. In theory, these can be combined to calculate height at centre of gravity (Equation 8.3), by assuming that the weight distribution of the stem and leaves across the whole stem length and the weight distribution of the ear are uniform. This method of calculation was tested in the lodging experiments, and then used to ascertain the relative importance of the components of height at centre of gravity. It was not used to predict height at centre of gravity over time.

$$X = \frac{(S_L S_W + 2S_L E_W + E_L E_W)}{2(S_W + E_W)} \qquad \textbf{(Equation 8.3)}$$

X - height at centre of gravity

S_L - stem height to ear base

S_W - stem and leaf fresh weight

E_L - ear length

E_W - ear fresh weight

It was shown in Chapter 5 that height at centre of gravity increased throughout the grain filling period and varied for different husbandry treatments. This variation was used to test Equation 8.3. In the MT95 experiment all the components of height at centre of gravity, except ear length, were measured weekly between GS 61 and GS 75 on the high and low risk treatments (with PGRs). A default value of 100 mm was used for ear length. Figure 8.5 shows that most of the observed variation in height at centre of gravity was accounted for by the method of calculation given in Equation 8.3. In addition, the best fit line was very similar to the 1:1 relationship which further illustrates the accuracy of this calculation. However, the method consistently overestimated height at centre of gravity by about six centimetres. This suggests that the weight distributions of the leaves and stem, or the ear, were not uniform. Since grains develop first from the middle florets of the ear, filling the most distal sites last,

it is likely that the ear weight distribution was uniform. This would mean that the weight of the stem and leaves was not uniform, with the base of the plant heavier than the top, during the period of observation. This is surprising since at this stage of development the leaves of the lower culm nodes will be senesced leaving the upper leaves to contribute more weight. Perhaps the bottom part of the stem contributes proportionally more weight to cause this effect. It is possible that this part of the stem is heavier because it must provide more structural support. The reason for this uneven weight distribution must be investigated and taken into account when improving Equation 8.3.

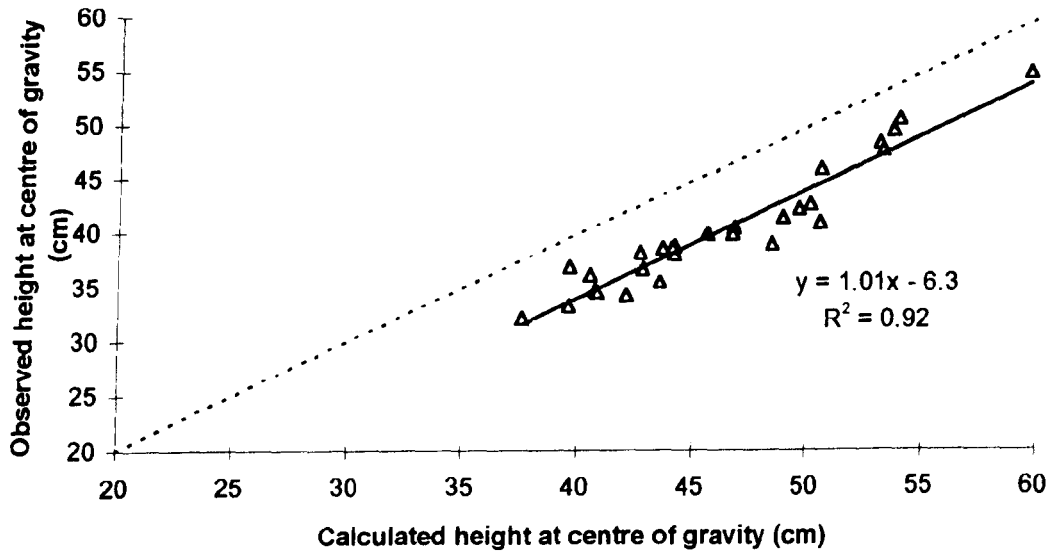

Figure 8.5 Calculated height at centre of gravity plotted against observed height at centre of gravity between GS 61 and GS 75 in the MT95 experiment. The ideal 1:1 relationship (---) and best fit line (—) are given.

The method of calculating height at centre of gravity has been used to determine its most influential components. This sensitivity analysis was based on the extreme values of stem height, stem and leaf fresh weight, ear fresh weight and ear length found in the MT95, VT95 and MT96 experiments. The range of ear length was estimated from ear area, which varied from 6 cm^2 to 12 cm^2 in the lodging experiments. Table 8.1 shows that stem height influences height at centre of gravity

most, with stem/leaf fresh weight and ear fresh weight moderately important and variation in ear length having a negligible effect.

Table 8.1 Results of sensitivity analysis for the components of height at centre of gravity based on the MT95, VT95 and MT96 lodging experiments.

	Default value	Range in lodging experiments	Predicted height at centre of gravity (cm)
Stem height (cm)	80	65 - 95	42 - 61
Stem/leaf fwt (g)	8.5	5 - 12	56 - 49
Ear fwt (g)	3	1.3 - 5	46 - 56
Ear length (cm)	8	6 - 12	51 - 52

It must be emphasised that the range of values used in this sensitivity analysis have only been taken from variety and husbandry experiments based at one site, during two seasons. The inclusion of other varieties, sites and seasons would be expected to stretch the ranges further.

The range for the most influential component, stem height, was mainly due to genotypic differences, and to a lesser extent, sowing date. Maximum stem height is reached at the beginning of anthesis, therefore only slight developmental changes are assumed for this character during the lodging risk period. The range of the moderately influential components stem/leaf and ear fresh weights were mainly due to developmental variation during grain filling. The patterns of development of these plant characters between anthesis and harvest have been described in Chapter 5, and could be used to help calculate the height at centre of gravity at any time during the lodging risk period. The two extreme husbandry treatments had a small influence on stem/leaf and ear fresh weights, although the effect of genotype has yet to be investigated. This suggests that understanding how these two plant characters change during the summer will be most important for predicting height at centre of gravity.

In summary, the most important component of height at centre of gravity is the stem length, which varies most due to genotype. Information about varietal heights is readily obtainable and could be used to help predict stem height. Sowing date also affects stem height and a prediction scheme which quantifies its influence must be developed. Height differences due to sowing date result mainly from variation in the number of extended internodes (Kirby *et al.*, 1985), and any prediction scheme will have to understand this mechanism. A cursory analysis of stem/leaf and ear fresh weights at harvest suggested that variation in these due to husbandry was small, resulting in a small influence on height at centre of gravity. However, further investigations, especially on other varieties, will be required to support this.

9. DISCUSSION

Research by Mulder (1954), Pinthus (1973), Graham (1983), Easson *et al.* (1993) and Crook and Ennos (1994; 1995) has shown that lodging risk is not only determined by the prevailing weather, but also by the state of the crop at the time of lodging. This provides strong support for the aim of controlling lodging. It has become apparent that lodging risk can be controlled to a certain extent by manipulating crop structure through careful husbandry decisions. As a result, guidelines for reducing lodging risk based mainly on husbandry factors have been developed (BASF, 1995; ADAS, 1996). However, widespread lodging still occurs. Important reasons for this appear to be poor identification of crops which are prone to lodging and a failure to recognise the likely type of lodging. This has resulted in the ineffective use of lodging controls. It is the aim of the 'Lodging Project' and of this thesis to test the hypothesis that spring crop observations may prove useful indicators of lodging risk. If this can be proven it will represent an important leap forward in lodging control, for not only will growers be able to influence lodging through husbandry, but they will also be able to predict its risk and type at a time when remedial action can be taken.

Evidence that early season growth, in terms of above ground dry weight, shoot number and canopy size, are indicative of lodging risk has been demonstrated in this project (Chapter 4). However, it was observed that gross differences in crop growth had often diminished or disappeared by the time lodging occurred. This suggests that these differences in crop growth were only indirectly linked with differences in lodging severity later in the season. It is likely that early season differences in crop growth influence the growth and development of other plant characters which are more directly linked with lodging. Investigating the effects of husbandry on the growth and development of plant characters directly associated with lodging tested this idea.

9.1 PREDICTING PLANT CHARACTERS ASSOCIATED WITH LODGING

Many plant characters have been associated with lodging, as described in section 1.2, and any of these could have been chosen for investigation in this study. The lodging-associated plant characters identified by the 'Lodging Project' include by order of their influence on lodging; root plate spread, stem diameter, shoot number per plant, structural rooting depth, stem failure yield stress, natural frequency, height at centre of gravity and stem wall width. This choice was based upon work by Baker *et al.* (Appendix 1) for several reasons: (i) the model of lodging developed by Baker *et al.* (Appendix 1) was the first to integrate the weather, plant and soil in a single model (ii) this meant a parametric analysis could be carried out to investigate the relative importance of each factor which influences lodging and (iii) tests showed this model to correctly account for lodging susceptibility in 82 % of crops. It is however acknowledged that development of this model is unfinished and flaws are likely to exist. Its potential inadequacies are discussed in section 9.2.2.

A reasonable indication of the summer-time values of root plate spread, stem diameter and shoot number per plant (the most important lodging-associated plant characters) can be gained using the spring-time prediction schemes developed in this study. Thus the hypothesis that assessments of the crop in spring can give an indication of lodging risk by estimating the summer-time values of plant characters associated with lodging appears to have been verified. As they stand these schemes will probably improve upon current assessments of lodging because they indicate potential anchorage failure moment, stem failure moment and plant base bending moment. This should give an indication of future lodging risk and lodging type which will enable lodging controls to be better targeted. Prediction schemes for the other lodging-associated plant characters are less important, yet are crucial if a precise and quantitative prediction of lodging risk is to be developed. Understanding of structural rooting depth, stem failure yield stress, natural frequency and height at centre of gravity has been greatly advanced, but further investigations are necessary.

9.1.1 Predicting anchorage

Plant population at GS 30 showed a reasonable (negative) relationship with the summer-time root plate spread. This relationship probably results from the plant's shade avoidance response which is likely to influence the length of rigid root and the width of the plant base Kasperbauer and Karlen (1986). It seems likely that this scheme will adequately account for large differences due to plant population, however smaller differences are unlikely to be accounted for. This will be important since small differences in root plate spread result in proportionally much greater differences in anchorage failure moment (Baker *et al.*; Appendix 1). This scheme must be tested with different soil types, seasons, varieties and with a wider range of plant populations. The latter could be very important since it is uncertain whether root plate spread will continue to increase for plant populations below 100 plants per metre squared. If root plate spread does have a maximum value, this would have large ramifications for the effect of seed rate on lodging risk because shoot number per plant can reach very high values at low seed rates (Darwinkel, 1978). This might cause root lodging risk to increase for very low plant populations.

Structural rooting depth remained almost constant from GS 30 to anthesis. Information cannot be found in the scientific literature to support or discount these observations. The relatively small developmental increase in rigid root length from GS 30 to GS 39 may have been expected to cause an increase in structural rooting depth. However, the developmental changes in the length of the rigid root appear to have had a negligible effect on structural rooting depth. It must be concluded that GS 30 measurements of structural rooting depth are the best way of predicting its summer-time values, but they will only detect large differences of at least ten millimetres. Large variation in this character prevented the modest differences due to sowing date and seed rate being predicted. However, it must be remembered that the differences due to husbandry were smaller than for root plate spread and therefore less important.

Root plate spread and structural rooting depth were very variable. This probably explains why spring measurements of root plate spread did not relate well with summer-time measurements and why GS 30 measurements of structural rooting depth only detected large summer-time differences. That this variation exists should not be a surprise. Lupton *et al.* (1974) suggested that soil and climatic conditions influence root growth more than genotype. The variation could be due to environmental conditions, such as localised differences in soil structure. Alternatively, it may be due to imprecise identification of the root plate spread and structural rooting depth. Measurement of root plate spread relied on the identification of the length of crown root which is rigid enough to hold a cone of soil. The rhizosheath was used as a guide for this. However, the point where the root ceased to be rigid was sometimes difficult to determine and at times may be regarded as subjective. Similarly the measurement of structural rooting depth relied on identifying the point along the stem at which it rose above the soil surface. This was difficult, particularly at later stages of plant development. More accurate methods for measuring root plate spread and structural rooting depth must be investigated in future work e.g. *in situ* measurements might be developed, or greater repetition employed, or the root rigidity might be considered. More precise measurements of root plate spread may enable the summer-time prediction of this plant character to be based on spring measurements of itself. Such a scheme may prove more accurate than relying on the indirect relationship between plant density and root plate spread.

Finally, root plate spread and structural rooting depth were positively related. This was probably due to the strong influence of rigid root length on both these characters as a result of the seed rate treatments. Further work could investigate this relationship with the aim of predicting one plant character from the other. This would reduce the number of spring measurements required to estimate lodging risk. However, it should be noted that these two plant characters are not influenced by the same component parts e.g. crown depth affects structural rooting depth, but not root plate spread. This will limit the accuracy of such a prediction.

9.1.2 Predicting stem failure moment

Plant characters used to calculate stem failure moment could not be measured before GS 33. Therefore, a prediction scheme at GS 30 must rely on substitute values. However, treatment differences in the stem characters could be detected as early as GS 33, and these were maintained until harvest. This suggests that accurate predictions of stem failure moment could be made by measuring the stem characters directly at GS 33 and 39, which would be in time for decisions on late PGR applications. To make these schemes quantitative the decrease in stem diameter and wall width from GS 39 to harvest (discussed below) must be accounted for.

In this study the decline in stem diameter and wall width reduced stem failure moment by half. Such an early and dramatic decrease in stem failure moment was not found by Crook *et al.* (1994), who showed that stem failure moment only started to decrease about one week before harvest. In this case the decrease was caused by a decrease in Young's modulus, which is an important component of failure yield stress. Crook *et al.* (1994) also showed stem diameter to decrease slightly between the beginning of June and early July, but this had a negligible affect on stem failure moment. The decline in stem diameter and wall width observed in this study could be due to loss of cell turgidity. Stems with large water contents have been shown to have greater strength and rigidity (Wainwright *et al.*, 1976). This may be investigated in future studies. Stem failure yield stress did not decrease which suggests that structural carbohydrates were not relocated during grain filling, in agreement with Schnyder (1993).

Substitute measurements were found to predict the stem characters at GS 30. It seemed likely that the consistent effects of early sowing, high seed rate and high residual soil nitrogen in reducing stem diameter, wall width and consequently stem failure moment were due to the greater number of shoots per metre squared and greater inter plant shading during stem extension. More shoots resulted in less dry matter partitioned to each developing stem, whilst greater interplant shading caused

more rapid stem extension (etiolation). This may explain why the weakest stems were often associated with a combination of these three husbandry factors, since together these factors usually generate a high shoot density and large canopy in the spring.

The quantitative prediction of stem diameter and wall width from spring shoot number and canopy size was very successful considering the disparity of the predictors and predicted plant characters and the number of assumptions used. The main obstacle preventing an accurate prediction appears to be obtaining a precise shoot number. This is difficult at GS 30 because shoots are often dying rapidly and potentially fertile ones are difficult to identify. Further work has shown a good relationship between canopy size and fertile shoot number at GS 30. Such a relationship could be used to gain a less variable measure of shoot number. This would also reduce the number of spring measurements which have to be carried out to predict lodging risk. Further work must be carried out to test whether this relationship holds in different environments and for different varieties.

Analysis of the scheme for predicting the stem characters suggests their variation is mainly due to variation in shoot number per metre squared, since this could vary two fold whereas variation in extension rate was much smaller. However, shoot number per metre squared at GS 30 bore no relation with the summer-time stem characters. Thus it appears that the influence of canopy size on stem extension rate and stem diameter is important. This is likely to be reinforced when the relationship between the P_{FR}/P_{TOTAL} ratio and stem extension rate is quantified. The response of stem extension rate to shade in wheat appears to be stronger than assumed in this study. Casal (1993) has shown that the range of R/FR ratios found within different sized crop canopies can double the rate of extension of the basal internode in wheat. Indirect evidence to support this was also found by this study.

One of the problems with predicting stem diameter and wall width is that their values change during the lodging risk period. It must be decided whether to predict the smallest value at harvest, or their value at the stage of development when lodging

would be most detrimental to grain yield, which would be during grain filling. Alternatively, an attempt could be made to quantify the rate of decline of stem diameter and wall width, which would allow their values to be predicted at any time during the greatest lodging risk period.

The material strength of the stem wall (stem failure yield stress) showed large variation and is directly proportional to stem failure moment (Baker *et al.*, Appendix 1). It is therefore an important plant character to predict. Quantifying the effect of genotype and investigating the effect of soil nitrogen supply will help predict this character. Its prediction proved difficult because much of its variation could not be accounted for. However, stem failure yield stress remained reasonably stable from GS 33 or GS 39 until harvest. Therefore measurements at this stage of plant development may prove useful for supporting decisions about mid window and late PGRs.

9.1.3 Predicting base bending moment

9.1.3.1 Final shoot number per plant

Differences in final shoot number per plant (due mainly to seed rate) at GS 30 were still present at harvest. It appears likely that a prediction scheme based on GS 30 measurements can be developed successfully. A prediction scheme based on plant number, the maximum shoot number and a model of tiller survival has proved very successful. This prediction demonstrated that plant population is crucial in determining final shoot number per plant. However, a number of limitations exist which must be recognised and the large proportion of variation accounted for by the prediction should not cause complacency. Shoot number per plant is a very variable character which has a large impact on lodging, as illustrated by the reduced per cent area lodged in the Canopy Management treatment. It is unlikely that the prediction scheme outlined in Chapter 8 would be as precise if it was tested for different genotypes, in more seasons and for a wider range of nitrogen supplies.

Genotype, nitrogen supply and incident radiation are known to have an important influence on shoot number per metre squared (Thorne and Wood, 1987). It is likely that the influence of nitrogen and radiation supplies during tillering are taken into account by measuring maximum shoot number. However, their effect on tiller survival is not taken into account. Reducing nitrogen supply during the period of tiller survival by between 60 and 120 kg ha^{-1} N in the Canopy Management treatment reduced shoot number per plant from an average of 4.0 to 3.5. A series of experiments studying the effect of nitrogen supply and time of application on shoot survival, and its interaction with genotype, will be required to incorporate this into a prediction. Radiation supply during tiller death cannot be predicted, therefore long term means of different sites would have to be used. A large quantity of data about genotypic effects on tillering can be obtained from existing data sets (e.g. Spink *et al.*, 1996).

9.1.3.2 Natural frequency and height at centre of gravity

Natural frequency and height at centre of gravity cannot be measured accurately before GS 39 which means that substitute plant characters must be found to develop a prediction scheme at GS 30. Baker (1995) suggests that height at centre of gravity is an important component of natural frequency. This study has shown that there is a strong inverse relationship between height at centre of gravity and natural frequency and demonstrates that, of the plant components known to influence natural frequency, height at centre of gravity is by far the most influential. It therefore seems reasonable to base the prediction of natural frequency on this relationship, especially given the complexity of natural frequency. It must be noted that natural frequency and height at centre of gravity develop differently throughout the lodging risk period and will therefore have different relationships depending at which stage of plant development they are measured. A solution may be to predict natural frequency at the growth stage when base bending moment is greatest, which occurs at the end of grain filling.

The observation that seed rate influences natural frequency but not height at centre of gravity suggests that the other components of natural frequency, such as stem stiffness and root ball resistance, should not be trivialised. A more expensive

alternative to predicting natural frequency from height at centre of gravity would be to quantify the idealised relationship given in Baker (1995) which relates natural frequency to height at centre of gravity, ear weight, stem stiffness and root ball resistance.

Height at centre of gravity was successfully calculated from stem height, combined stem and leaf fresh weight, ear fresh weight and ear length. The results of a cursory parametric analysis showed that if developmental variation in these components is ignored then stem height has the greatest influence on height at centre of gravity. This explains why crop height has traditionally been closely associated with lodging risk (Sylvester-Bradley and Scott, 1990). That the developmental variation of ear weight and stem and leaf fresh weight is ignored is justified by assuming that only a prediction of the greatest height at centre of gravity is required. Thus it appears that a prediction of stem height will be extremely valuable for estimating height at centre of gravity and natural frequency, which are two of the most important inputs for the calculation of shoot base bending moment.

9.1.3.3 Predicting stem height

It was the aim of this study only to elucidate factors which were important in natural frequency and height at centre of gravity. Therefore a scheme for the prediction of stem height has not been developed. However, an outline for a future prediction scheme can be considered. Stem height is a function of the number of extended internodes and internode length (Kirby *et al.*, 1985a; Stapper and Fisher, 1990). Development and growth are the two processes which affect the components of height, with development exerting the greatest influence (Kirby, 1994; Stapper and Fisher, 1990). Etiolation is the non-developmental process which affects internode length. For a particular variety, height variation has been most closely associated with the number of extended internodes (Stapper and Fischer. 1990). Sowing date appeared to strongly influence the number of extended internodes. Internode and leaf development are closely co-ordinated (Kirby, 1988). The number of extended internodes will be directly related to the number of leaves yet to emerge when stem

extension begins (Kirby, 1994), which is usually between the stages of double ridges and terminal spikelet (Kirby, 1994). The number of leaves to emerge can be observed by dissecting the plant at the start of stem extension (GS 30). Alternatively, the number of leaves to emerge at the beginning of stem extension can be estimated theoretically (Kirby, 1994; section 2.3.2.1).

The length of individual internodes depends on the duration and rate of their extension. The duration of internode extension is the most important factor in determining internode length (Stapper and Fisher, 1990). An internode extends for a set thermal time of approximately 1.5 phyllochrons (Kirby, 1994). Phyllochron length is affected by sowing date and variety (Kirby, 1994; Kirby *et al.* 1985b). By observing or calculating phyllochron length an estimate of the duration of internode extension may be obtained. Quantitative information about the extension rate of individual internodes is rare. The extension rate of successive internodes increases, with the peduncle extending at about twice the rate of the lower internodes (Kirby, 1988). Also, internode extension rate is known to vary due to light quality (Casal, 1993), with poor light quality causing rapid stem extension (etiolation). This has been modelled in an earlier prediction scheme for the basal internodes (Chapter 7), but it is uncertain whether this can be applied to the distal internodes.

In summary, the number of extended internodes and the thermal duration of internode extension can be estimated at or before stem extension by counting the number of leaves to emerge at GS 30 and recording the thermal duration between successive leaf emergence. Alternatively, by using models developed by Kirby (1994) for the prediction of 1) final leaf number on the main shoot, 2) the relationship between the number of leaves to emerge at double ridges/terminal spikelet (start of stem extension) with final leaf number and 3) the rate of leaf emergence (phyllochron), the number of extended internodes and their duration of extension can be predicted. Difficulty arises when predicting internode extension rate because it varies with successive internodes and light quality within the canopy. Extension rates for the

four most distal internodes from Kirby (1988) could be used. The stem extension rate and light quality model outlined in Chapter 7 could modify these values.

9.2 APPLYING THE PREDICTION SCHEMES

If growers are to accept and take up this new method of assessing lodging risk then the measurements required must be both quick and inexpensive and they must deliver a reliable estimate of lodging risk.

The spring measurements required for the prediction schemes developed so far include plant number per metre squared, shoot number per metre squared, green area index and structural rooting depth. These can be assessed quickly and easily in the field without any specialised equipment. It is envisaged that at the beginning of stem extension, assessments of lodging risk may be done on an individual field basis to allow the most suitable remedial controls to be applied to each field. Assessments may also be carried out in different parts of the field, such as its margin and centre. This could pave the way for treating parts of the field with the greatest lodging risk differently.

The reliability of the assessment of lodging risk depends upon the accuracy and precision of the spring measurements, the reliability of the spring prediction schemes and the reliability of the lodging model. Growers will require training as to how to measure the spring plant and crop characters, and how to take representative samples. Sample sizes must be carefully chosen to ensure maximum precision with minimum time spent. For example, more assessments should be made of structural rooting depth and shoot number, which are very variable, and fewer assessments of green area index and plant population.

9.2.1 Reliability of the prediction schemes

The reliability of individual prediction schemes have been discussed in section 9.1, however some general limitations also exist. These are that the prediction schemes have been developed or tested at one site, with one variety in only two seasons. Soil

type is the most important site difference which has not been tested. ADAS Rosemaund has a water retentive fertile soil, which is similar of the soil on which large areas of wheat are grown in the UK. However, in the region of 20% of wheat is grown on drought prone soils which are less fertile (Foulkes *et al.*, 1994)). These soil types usually produce smaller biomass crops with different crop structures compared with those grown at ADAS Rosemaund. Such differences are not accounted for by the prediction schemes, which may reduce their accuracy.

Rosemaund has a similar climate to the main wheat growing areas in England. However, applying the prediction schemes to Scotland where the temperatures are cooler and the length of the wheat growing season is longer may present difficulties. The two testing seasons were very different, the first having a very mild winter followed by a warm dry summer and the second having a much colder winter followed by a cold May and a wetter summer. These conditions produced different crop structures and provided a reasonable test bed for the prediction schemes. However, it is recognised that testing would be required in more seasons.

Genotype had a large influence on all the lodging-associated plant characters. It is hoped that the basic principles of each prediction scheme will apply for different genotypes, although this must be tested. It seems likely that prediction schemes may have to be individually calibrated for different varieties. This problem will be perennial since varieties commonly remain in the NIAB recommended list for as little as three years. Therefore a method of quickly typing new varieties must be developed.

9.2.2 Reliability of the lodging model

A number of assumptions have been made in the lodging model which could affect its reliability. Most importantly the lodging model assumes that the unit of stem lodging is the individual shoot and the unit of root lodging is the whole plant. This is unproven, but seems to be the most likely mechanism by which stem and root lodging occur. However, it is possible that the unit of stem and root lodging could be a group

of plants, or the unit of root lodging could be an individual shoot. Additionally no account is made of lodged plants leaning on standing plants, which could cause lodging by a 'domino' effect. The model also assumes that wheat crops are homogeneous. However, crop characteristics vary within fields. For example, lodging is observed to occur more frequently within the field margins (Berry *et al*, 1998). Finally, this study has only investigated the characteristics of main shoots, with lower order tillers assumed to have similar characteristics. This is unlikely to be true since low order tillers have been shown to have smaller grain yields and smaller straw dry weights than main shoots (Thorne and Wood, 1987). Failure to recognise these factors is likely to reduce the accuracy of the lodging model. Future work is required to investigate the exact mechanism of lodging and to modify the model so that it accounts for spatial non uniformity of the crop. Changes in the lodging model to incorporate any of these factors could also influence the plant characters which have been deemed important in lodging by this study.

Limitations also exist for the calculation of anchorage failure moment, base bending moment and stem failure moment. These could also reduce the reliability of the lodging model and must be discussed. The calculation of anchorage failure moment, based on the theoretical model of Crook and Ennos (1993), has been calibrated in experiments of the 'Lodging Project'. For a given root plate spread the anchorage model of Baker *et al.* (Appendix 1) gives an anchorage failure moment which is about half that found in experiments by Crook and Ennos (1993). This difference is due to different methods of measuring root plate spread ('root cone' diameter), hence differences in the volume of soil held and rotated. Crook and Ennos excavated the root cone (with attached soil) from a saturated soil core to measure the root cone diameter. The method of Baker defined the root cone diameter by the point at which the crown root abruptly became thinner, more flexible and no longer had a dense covering of root hairs to which soil adhered (rhizosheath). The method of estimating root plate spread of Crook and Ennos is likely to be more accurate than the method of Baker. However, the method of Baker is much more suitable for easy and rapid field

measurements, when the soil is seldom saturated to allow the other method to be used.

The importance of root rigidity in anchorage has been noted by Easson *et al.* (1995); it also varies due to genotype (Crook and Ennos, 1994). The fact that this rooting character is not taken into account by the anchorage model of Baker could be important and further research is required to quantify its influence on anchorage. It has been suggested that the number of supporting roots per stem is an important factor in anchorage (Easson *et al.*, 1993). The method of Baker assumes that enough crown roots will be present to support a cone of soil. Experiments in this study have shown that most plants have at least 20 crown roots (Griffin, 1998), which would be expected to be sufficient for containing a cone of soil. However, on occasion as few as six roots per plant have been observed. Such low root numbers might affect the ability of the root cone to support any soil, and should be taken into account in further model development. Finally, the method of Baker does not take into account the observation that basal internodes cut a slot through the surface of the soil during root lodging. The method of Baker assumes that the plant base is the width of a single stem and therefore offers little resistance to root lodging. However, this study has found that plants with large numbers of stems have plant bases up to 12 mm wide which would be expected to offer significant resistance to anchorage failure.

The dynamic model used to predict the shoot base bending moment is based on work of Baker (1995) and its application to isolated and forest trees suggests it is reasonably realistic. The principal inputs include the natural frequency and height at centre of gravity of the main shoot. Other inputs include ear area, turbulence intensity, damping ratio, turbulence length scale and ear drag coefficient. At the beginning of this study the values of these parameters were not well specified and it was uncertain how large an influence they had on shoot base bending moment. However, recent work by Baker *et al.* (Appendix 1) suggests that ear area, turbulence intensity and ear drag coefficient may have an important influence. Further work in developing the lodging model and prediction schemes should take these into account.

Traditionally, stem height (Fielder, 1988) and final biomass (Green and Ivins, 1985) have been perceived as important factors influencing lodging. However, alone these plant characters are not a reliable guide of a plant's leverage and lodging risk e.g. some short strawed varieties have poor standing powers (NIAB, 1996). This model accounts for the way these plant characters relate to lodging more correctly by using height at centre of gravity and natural frequency,

The method used to calculate stem failure moment appears to be based on structurally sound principles. Furthermore two of its components, stem diameter and wall width, have been cited by Pinthus (1973), Neenan and Spencer-Smith (1975), Easson *et al.* (1993) and Crook and Ennos (1995) as important factors influencing stem failure moment. Stem stiffness is often quoted as an important component of stem strength. This plant character is accounted for in the method of Baker as it is one of the components of stem failure yield stress. Stem stiffness also affects the 'springiness' of a shoot, and therefore affects the shoot's base bending moment. This effect is taken into account by natural frequency.

In general, the lodging model of Baker may be regarded as a prototype method for calculating lodging risk which is based on scientific principles and which takes into account most plant characters traditionally associated with lodging. Potential lodging-associated plant characters not accounted for are root rigidity, root number, plant base width and some aerodynamic characteristics of the canopy. As it stands, it gives a reasonable estimate of lodging (Baker *et al.*, Appendix 1) and will be reasonably reliable, but it is recognised that further development and testing of the model is required to improve and confirm its reliability.

9.2.3 Summary

All stages of the prediction of lodging risk have a degree of error associated with them, some greater than others. What happens when these errors are combined ? Will the error associated with the predicted lodging risk be too great to allow the prediction to be useful ? It is likely that during the early stages of development the

error will be quite large and advice based on it must be tentatively given. However, when it is considered that the majority of growers are not certain about how lodging occurs, even very general information such as whether or not a crop is likely to root or stem lodge will be valuable. As the parts of the prediction schemes and lodging model are tested and improved this error should decrease to allow more refined advice to be given, such as the timings and rates of PGRs.

9.3 IMPLICATIONS FOR THE FARMING INDUSTRY

The hypothesis that early season crop observations can give an indication of lodging risk has been proven. Furthermore the likely cause of lodging can be predicted. This study strongly suggests that an effective prediction scheme of lodging risk can be set up based on the lodging model of Baker *et al.* (Appendix 1) and an understanding of the development and growth of lodging-associated plant characters. This scheme will be based on crop measurements taken by the grower at the beginning of stem extension together with other field observations. The framework for the prediction scheme has been set up in this thesis, but more work is required to develop and test it. Information from this study will help to reduce lodging by encouraging growers to assess lodging risk in the spring, by more effective use of lodging controls, by improvements in husbandry strategy for the production of sturdy crops and by helping breeders to better select for lodging resistant varieties.

9.3.1 Lodging control

An assessment of lodging risk can be done simply and quickly by measuring a few crop characters in the spring. The assessment will allow lodging controls to be targeted only at crops with high lodging risk. It will also mean that lodging controls can be applied in amounts which are commensurate with the severity of lodging risk, e.g. no lodging control for a crop with low lodging risk, a single application of chlormequat for a crop with moderate lodging risk, or an application of chlormequat followed by Terpal for a crop with high lodging risk. Furthermore, specific lodging controls could be chosen to counter the different causes of lodging, e.g. spring rolling might be most appropriate for a crop prone to root lodging due to weak anchorage;

reduced spring nitrogen for a crop prone to stem lodging due to weak stems caused by a large spring canopy; or PGRs might be the most effective way of reducing lodging risk of a crop with a high base bending moment.

The lodging risk of crops is often assessed from the size (top heaviness) of its canopy. As a result much faith is placed on PGRs for the successful reduction of lodging risk. However, the expectations of plant growth regulators are often not realised. Our investigations have shown that the aerial forces imposed by the canopy on the plant base are less important in determining lodging than variation in stem and anchorage strength. This may explain the poor lodging control which is often found after the application of PGRs.

An effective lodging control chemical must not only reduce leverage, but must also strengthen anchorage and the stem base. Some PGR manufacturers already claim these properties in their products, but this is not always supported by the scientific literature (Crook and Ennos, 1995). It is possible that these products do not always influence the plant characters associated with stem strength and anchorage strength. For example, a claim for increased 'rooting' does not necessarily mean the structural roots and anchorage are being maximised because it may refer to an improvement in the distal non-structural parts of the root system. Thus, chemical manufacturers must aim to manipulate the important lodging-associated plant characters, particularly the spread and depth of the root plate. That this can be achieved is demonstrated by the seed treatment 'Baytan', which increases crown depth by shortening the sub-crown internode (Montfort *et al.*, 1996).

9.3.2 Growing sturdy crops

This study has also shown that lodging risk can be reduced most effectively by taking the correct decisions at sowing. Remedial controls in spring are less effective at reducing lodging risk, and in some cases cannot reduce the risk of a poorly managed crop enough to prevent lodging Nevertheless, in most cases they certainly reduce lodging risk and often make the difference between a crop lodging or not lodging.

Mechanisms by which husbandry affects lodging have been further elucidated. Early sowing not only increases lodging risk by increasing shoot base bending moment, it also reduces stem failure moment due to the large spring canopies it often produces. Large seed rates increase root lodging risk by reducing root plate spread and anchorage, contrary to perceived wisdom the effect on stem height and shoot base bending moment is minimal. High levels of residual soil nitrogen increase stem lodging risk by reducing stem diameter and stem failure moment; again the effect on stem height and shoot base bending moment is small. Knowledge of how these factors affect lodging will help growers choose cropping strategies which pre-empt potential causes of lodging, e.g. crops could be sown later to counter potential weak stem bases in crops sown on fertile soil, or seed rates could be cut to counter potential poor anchorage due to weak soil strength. The experiments have shown these types of early decisions to be very effective and inexpensive methods of lodging prevention.

The production of sturdy crops may be expected to compromise grain yield due to later sowing, the use of reduced seed rates and smaller nitrogen applications. This need not be the case. This study has shown that the golden rules for avoiding high lodging risk crops are to avoid spring crops with dense plant populations and large canopies. It should be possible to grow crops with a high yield potential without producing these undesirable spring characteristics. For example a crop may be sown early to generate a high yield potential, but the large spring canopy associated with early sowing could be limited by sowing less seeds and applying nitrogen later in the spring. Experiments in the Lodging Project have demonstrated that seed rates can be reduced and the application of nitrogen delayed without reducing grain yield.

Interestingly, the values for plant characters associated with lodging could be stretched more by agronomic decisions such as sowing date, seed rate and nitrogen applications than by choice of variety. Given the large range in standing powers of the varieties tested, this further highlights the potential for reducing lodging risk

through crop management decisions, and strongly suggests that the development of precise guidelines for growing lodging resistant crops will be valuable.

9.3.3 Lodging resistant varieties

Plant characters which influence lodging have been identified. This will allow variety testers to gain a better estimate of a plant's lodging susceptibility without relying on the occurrence of lodging. Furthermore, the most likely type of lodging to which individual varieties are prone may be identified. This will allow growers to target the most appropriate lodging controls at each variety. Growers will also be able to match varieties with expected environmental conditions, e.g. strong stemmed varieties should be grown on soils with high levels of residual nitrogen.

Plant breeders may use the lodging-associated plant characters to choose lodging resistant varieties more efficiently. Previously the anchorage and stem strength properties have often been neglected in the selection process. This study has demonstrated that the components of anchorage strength, root plate spread and structural rooting depth; and the components of stem strength, stem diameter, stem wall width and failure yield stress have large genotypic variation. This investigation was on relatively few varieties which suggests there could be even greater genetic variation from which varieties with strong anchorage and strong stems can be selected.

Stem failure moment is greatest from GS 39 to early grain filling, after which it decreases considerably. Anchorage failure moment remains relatively constant throughout the lodging risk period. It appears that between ear emergence and grain filling, when loss of grain yield due to lodging is greatest (Fischer and Stapper, 1987), root lodging will be more likely than stem lodging. Whilst not suggesting that stem lodging is unimportant, root lodging is more likely to lead to the largest yield losses and this emphasises the need to maximise crop anchorage, either by rolling, reducing seed rate or varietal choice.

9.4 FUTURE WORK

1) Test and further develop the predictions set up in this study. The details of the improvements required for each prediction scheme have been described in Chapters 6 to 9, but testing the schemes in a wider range of sites, seasons, varieties and husbandry practices will be imperative.

In addition, to develop prediction schemes of lodging risk at stages of development other than GS 30, e.g. remedial action can be taken up to GS 45 and it would be expected that more accurate predictions of lodging risk could be made using crop information taken closer to the date of latest remedial action. On the other hand, soil consolidation by spring rolling has been shown to be a potentially important control measure (Crook, 1994). However, this should be done before GS 30, necessitating an earlier prediction of lodging risk.

2) Design a protocol for growers which outlines how to measure spring-time plant characters indicative of lodging. Particular emphasis should be placed on describing the measurement of the structural rooting characters.

3) Test and further develop the lodging model. Particularly to ensure the model correctly accounts for the mechanism of stem and root lodging and makes allowances for crop non uniformity. Also to improve understanding of the role of root plate spread and root rigidity in the anchorage model, and to quantify important parameters in the base bending moment model, such as drag coefficient.

4) Identify the lodging-associated plant characters as varietal traits. This will enable the assessment of varietal standing power to be based on plant characteristics rather than relying on the occurrence of lodging. Plant breeders may also use the lodging-associated plant characters to select for lodging resistant varieties more effectively.

5) Design husbandry guidelines for the reduction of lodging risk, whilst still optimising yields. Specific guidelines should be developed which are able to counter high lodging risk caused by different reasons, e.g. high rainfall or windy sites, historically large crop growth, weak soil strength and specific varietal weaknesses (weak anchorage or weak stems).

6) Develop a model for lodging in other cereals such as barley and oats. Lodging is more prevalent in barley and oats, and quality is as (or more) important, e.g. malting barley. It is likely that the lodging model of Baker *et al.* (Appendix 1) can be adapted for both these cereals, although a modification to account for the oat panicle may be required. However, these cereals differ greatly in their physiology, which would mean that new prediction schemes would need to be developed.

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APPENDIX 1

A method for the assessment of the risk of wheat lodging

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Summary

A model of the wheat canopy/root/soil system has been developed, which calculates the risk of stem and root lodging from crop parameters and soil characteristics. For a large number of wind speed and rainfall realisations the model determines whether or not stem lodging will occur by comparing the wind induced bending moment at the base of an individual shoot with the stem base failure moment. Similarly, whether or not root lodging will occur is ascertained by comparing the wind induced base bending moment of the whole plant with the plant's root failure moment. The overall probability of lodging is determined from the proportion of wind speed and rainfall realisations for which lodging is predicted to occur.

For differently managed wheat crops the model correctly predicted lodging in 21of the 30 lodged crops and nil lodging for 38 of the 42 standing crops. The model showed that both stem and root lodging may occur given suitable circumstances. The state of the crop was as important as the prevailing weather for influencing lodging risk. A relatively small number of crop parameters were of major importance in the lodging process. These include the shoot's centre of gravity height, natural frequency, stem base radius and failure yield stress, and the plant's shoot number, root plate diameter and structural rooting depth. In addition, the importance of soil, particularly clay content, in influencing anchorage was illustrated. Recommendations for further improvement of the model include improvement of the soil strength calculation.

1. Introduction

Lodging is the state of permanent displacement of cereal stems from their upright position (Pinthus, 1973). There are two possible points of failure in the plant's structure, the stem and the root. The elongated stem consists of a series of jointed hollow internodes connected by solid swollen meristematic nodes. The stem is strengthened by lignin, but may fail due to bending or buckling of the lower stem internodes (Neenan and Spencer-Smith, 1975). Root lodging results from a failure in root-soil integrity so that straight, unbroken culms lean or fall from the crown (Graham 1983). Lodging in cereals generally occurs during the two or three months preceding harvest and can drastically reduce profitability through reduced yield, delayed harvest, increased grain drying costs and reduced grain quality. Yield losses of up to 45% have been observed (Weibel & Pendleton, 1964; Laude & Pauli,1956; Mulder, 1954; Fischer & Stapper, 1990). In the severe lodging year of 1992, it has been estimated that lodging in winter wheat (*Triticum aestivum* L.) cost the farming industry up to £130 million through loss of yield alone (Berry *et al.*, 1998). Also in this year, lodging reduced the grain quality standard (Hagberg falling number) from a UK five year average of 287 to 254 (HGCA, 1993).

Plant growth regulators (PGRs) used to control lodging, often have to be applied as an 'insurance measure'. For example, in 1994 lodging was not widespread but 74% of the UK wheat area was treated with PGRs at a cost to cereal growers of £9.9 million (Garthwaite, Thomas & Hart, 1994). On the other hand, in years of severe lodging, the application of PGRs has not prevented lodging completely (Woolley, 1992). Hence there is a need to understand more fully how lodging risk is influenced, to enable control measures to be targeted more

effectively.

It is clear that weather plays an important part in determining lodging risk, but there is little published information quantifying the weather conditions necessary to cause a lodging event. Easson, White & Pickles (1993) observed that lodging occurred gradually over a period of 24 hours during which rain fell and that it could occur with low wind speeds. Lodging was also found to be more closely associated with the occurrence of rainfall than the amount of rainfall. Lodging risk is strongly influenced by cultivar and husbandry factors including sowing date, seed rate, drilling depth and rate of nitrogen application, as well as the application of PGRs (Pinthus, 1973; Sylvester-Bradley & Scott, 1990). We envisage that the influence of these factors on lodging risk is through their ability to alter crop structure but, to date, few studies have been carried out which interrelate the facets of structure that alter lodging risk. The interactions between weather, cultivar, and husbandry appear to confer a complexity on the lodging process that makes a proper understanding of its control very difficult.

In this paper an attempt has been made to understand these complex interactions through the development and calibration of a model describing the lodging process. The model assumes that the dominant parameter that affects lodging is the wind induced bending moment at the stem base. The value of this bending moment relative to the failure moment of the stem, and the failure moment of the root/soil system indicates whether or not lodging of either type will occur. A fundamental assumption is made that the unit of stem lodging is the individual shoot, and that the unit of root lodging is the whole plant. This must be regarded as an unproven, if reasonable, hypothesis.

The following section presents an outline of the method used to develop the lodging model. This is followed by a more detailed description of the components of the model, and a parametric investigation in which the various model parameters are systematically varied to demonstrate their individual effects. Finally the results of the parametric investigation and its implications for the farming industry are discussed and concluding remarks made. It is envisaged that two related papers will be submitted for publication in the near future, the first of which will present detailed agronomic experiments carried out to measure the lodging risk of wheat varieties grown by different husbandry methods, and the second which will present data for crop development throughout the growing season up to and including the lodging period. Preliminary considerations of these aspects of the investigations are given in Berry *et al.* (1998) and more fully in a PhD thesis (Griffin, 1998). Both these papers will use the model described in the present paper as a basis of discussion. With further work, this method could provide a basis for quantitative prediction of lodging risk, and thence improvement in its control and of crop profitability.

2. Outline of the method

A flow chart of the lodging risk assessment method is given in Fig. 1. The overall aim of the method is to predict the probability of stem lodging and root lodging at any one site in a particular lodging season. For the site in question it is necessary to provide data on the wind, rain, soil and

expected plant characteristics during the peak lodging period in July. The daily maximum hourly mean wind speed and daily rainfall probability distributions are then calculated from the wind and rainfall characteristics of the site. A Monte Carlo simulation technique is then used to generate a series of 1000 hourly mean wind speeds and daily rainfalls that are consistent with the calculated probability distributions. For each wind speed/rainfall data pair, the degree of soil saturation, soil shear strength and plant natural frequencies are then calculated, these parameters being fundamental in determining the plant's dynamic characteristics and lodging resistance. The method of Baker (1995) is used to calculate the extreme stem base bending moment that would be expected with the simulated wind and rain conditions. The stem failure moment and root failure moment are calculated using simple principles of structural analysis and a simplified version of the root strength model of Crook & Ennos (1993). A comparison of these three moments then enables the occurrence of stem and root lodging to be ascertained for each wind speed/rainfall data pair. The total number of occurrences of both lodging types is then divided by 1000 to give a probability of lodging for any one day. The probability of lodging during any one peak lodging period (40 days centred on mid July) is then calculated. This period is used because it approximately coincides with the period of grain filling when lodging risk is greatest and yield penalties due to lodging are most severe. It is however acknowledged that lodging can occur before and after this period. The individual components of the method are considered in more detail in the next section.

3. Components of the model

3.1 WIND PROBABILITY DISTRIBUTION AND WIND SPEED PREDICTIONS

The first question that arises is what definition of wind speed should be used. As shown below the gust speed likely to cause lodging is calculated from the mean hourly wind speed. It will also be seen in the next section that it is appropriate to use daily average rainfalls to predict the ground conditions. Thus what is ideally required is the probability distribution of the maximum hourly mean wind speed that can be expected to occur in any one day. Data for this parameter is not directly available, but compilations of data are available for the probability distribution of hourly mean wind speeds at any one site and these can be used to attain the required distribution. The probability p_w that this hourly mean wind speed will exceed a certain value V is given by the Weibull distribution

$$p_w = e^{-k_1 V^{k_2}} \tag{1}$$

where k_1 and k_2 are site dependent constants. If, for the site in question, the value of V that is exceeded 50% of the time is V_{50} and the value that is exceeded 1% of the time is V_{99} one may write:

$$0.5 = e^{-k_1 V_{50}^{k_2}} \tag{2}$$

$$0.01 = e^{-k_1 V_{99}^{k_2}} \tag{3}$$

Thus if V_{50} and V_{99} are known, k_1 and k_2 may be found. Values of these velocities, ten metres above ground level in open countryside, at sea level conditions, V_{50}' and V_{99}', are given by various

compilations of Meteorological Office data (e.g. Cook (1985)). To attain values of V_{50} and V_{99} of relevance to the lodging problem, V_{50}' and V_{99}' must first be transformed with correction factors to allow for the difference between hourly mean wind speeds and daily maximum hourly mean wind speeds. They must then be further transformed to account for height above ground level, the altitude of the field in question (h m above sea level) and for seasonal conditions (i.e. July).

The expressions that are adapted are

$$V_{50} = 1.6 \times V_{5'0}\left(\frac{\ln(1/z_0)}{\ln(9/z_0)}\right)(1+0.0007h) \times 0.71 \qquad (4)$$

$$V_{99} = 1.15 \times V_{9'9}\left(\frac{\ln(1/z_0)}{\ln(9/z_0)}\right)(1+0.0009h) \times 0.71 \qquad (5)$$

The factors 1.6 and 1.15 transform the values of hourly mean wind speed to the equivalent values of daily maximum hourly mean wind speed, and have been attained by the authors from an analysis of several years data for a number of Meteorological Office sites. The logarithmic terms describe the well known logarithmic velocity profile and transform the velocity from a height of ten metres above ground level (or nine metres above the effective ground level, the top of a typical wheat canopy being one metre) to a value two metres above ground level (or one metre above the canopy top). z_0 is the surface roughness length. The reason for choosing to specify the velocity one metre above the canopy top is because it is known that wind loading of individual plants is due to large gusts from above the canopy penetrating through the top of the canopy. Thus it seems reasonable to specify wind gusts one metre above the top of the crop. The expressions in h

represent the altitude corrections as given by Cook (1985). The 0.71 factor, also given by Cook (1985), allows for the fact that wind speeds in July are significantly smaller than average annual values.

Once k_1 and k_2 have been determined from equations 1 to 5, a value of V, now interpreted as the daily maximum hourly mean wind speed, can be obtained from:

$$V = (-ln(p_w) / k_1)^{1/k_2} \tag{6}$$

and a randomly generated value of p_w between 0 and 1.

3.2. RAINFALL PROBABILITY DISTRIBUTION AND RAINFALL AND SOIL SATURATION PREDICTIONS

The next question that arises is what rainfall period is relevant to the lodging process. Intuitively one would expect that lodging would be dependent upon both short duration high intensity rainfall (of about one hour), and also by long-term rainfall conditions (average monthly rainfalls). As a compromise the lodging model uses daily rainfalls as its basis for the determination of soil saturation conditions. Note firstly that antecedent soil moisture is not taken into account, on the assumption that the top few centimetres of soil, which are of relevance to lodging, dry out very quickly and are usually in a dry condition. Secondly no account is taken in the model of the effects of evapotranspiration in reducing the amount of moisture in the soil or of the effect of plant interception. It is assumed that during lodging periods, when the weather is usually overcast and wet, evapotranspiration will be small, and that over one day most of the rain that falls will find its way onto the ground surface.

Shaw (1983) shows that the probability of the average daily rainfall exceeding a value i is given by p_r, where p_r is given by:

$$p_r = e^{-k_3 i} \tag{7}$$

k_3 can be found from meteorological data for the daily rainfall that is exceeded 50% of the time, i_{50}, since:

$$0.5 = e^{-k_3 i_{50}} \tag{8}$$

Thus a realisation of the daily rainfall can be obtained from a randomly generated value of p_r between 0 and 1 and

$$i = -\ln(p_r)\ k_3 \tag{9}$$

Once a value of i has been calculated, the surface layer of the soil is taken to be at field capacity if

$$i > l\,(f - w)\,\frac{\rho_s}{\rho_w} \tag{10}$$

where l is the crop structural rooting depth, f is the soil water content by weight at field capacity, w is the soil water content by weight at the permanent wilting point, ρ_s is the density of soil and ρ_w is the density of water.

3.3. DETERMINATION OF NATURAL FREQUENCY

The natural frequency of the canopy/root system n, can be expected to be a function of the wetness of the soil, with n decreasing in wet conditions due to the loosening of the soil around the roots. On the basis of limited experimental data (*unpublished*) the value of natural frequency in saturated conditions n_W is taken as $k_4\, n_D$ where n_D is the value in dry conditions and $k_4 = 0.8$. For soil conditions between permanent wilting point and field capacity the method assumes that

$$n = n_D - \frac{i}{\frac{\rho_s}{\rho_w}(f - w)\, l}(n_D - n_w) \tag{11}$$

3.4. CALCULATION OF GROUND STRENGTH

The ground shear strength s for a wet soil at field capacity s_w is given by

$$s = s_w = (1484\, e^{-5f/c}) \left(\frac{76.7 - 8.39v}{76.7 - 8.39\, v_R}\right)\left(\frac{47c - 2.94}{47\, c_R - 2.94}\right) \tag{12}$$

Here c is the clay content by weight and v is a visual score for soil structure (MAFF 1982), which is a measure of soil compaction in terms of the proportion of macro pores in the top 20cm of the soil. A soil with a visual score of zero has very few macro pores and is very compacted and strong. A soil with a visual score of ten has many macro pores and is uncompacted, friable and weak. c_R

and v_R are 'reference' values of c and v. This equation was derived from a variety of sources. The term in the first bracket relating soil strength to water content at field capacity was derived from data collected during the experiments reported in Griffin (1998). Note that this data was all obtained for a clay content of 0.27. The second term relating soil strength to visual score is taken from MAFF (1982), whilst the third relating soil strength to clay content is taken from Guerif (1994). If reference values of v_R =5 and c_R = 0.27 are taken, equation 12 reduces to:

$$s = s_w = (1484\, e^{-5f/c})(2.20 - 0.24v)(4.82c - 0.30) \qquad (13)$$

For dry soil at permanent wilting point *(i = 0)* the soil strength s_D is taken to be given by a similar expression

$$s = s_D = 1125\, e^{-5w/c}(2.20 - 0.24v)(4.82c - 0.30) \qquad (14)$$

For values of *i* between 0 and l(f - w) ρ_s / ρ_w the shear strength is taken to be given by:

$$s = s_D - \frac{i}{\frac{\rho_s}{\rho_w}(f - w)\, l}(s_D - s_w) \qquad (15)$$

i.e. a linear variation of s with i is presumed.

3.5. CALCULATION OF STEM BASE BENDING MOMENT

Once values of V and n have been obtained the value of the base bending moment for one shoot can be obtained from the method of Baker (1995) for plants within canopies. This gives B as

$$\frac{B}{1/2\delta AC_D V_g^2 X} - (1 + \frac{g}{(2\pi n)^2 X}(1 + e^{-\pi\delta}\frac{\sin(\pi/4)}{\pi/4}) \tag{16}$$

where ρ is the density of air, A is the ear area, C_D is the drag coefficient, X is the centre of gravity height of a shoot and δ is the plant damping ratio. V_g is a gust velocity and is related to the daily maximum hourly mean velocity V by the expressions of Greenway (1979)

$$\frac{V_g}{V} = 1 + \frac{\sigma_v}{V} L \tag{17}$$

where

$$L = J_1 g_v \tag{18}$$

and

$$g_v = \sqrt{2\ln(J_2 nT)} + 0.577 / \sqrt{2\ln(J_2 nT)} \tag{19}$$

$$J_1 = 1 - 0.1925((2n^x L_v / V) + 0.1)^{-0.6792} \tag{20}$$

$$J_2 = (n^x L_v / V)^{-1} (0.0066 + 0.2130 (2 n^x L_v / V))^{-0.6543} \quad (21)$$

σ_v V is the turbulence intensity taken as 0.5 at the crop height (Finnigan, 1979), ^xL_v is the turbulence length scale at the height at which the velocity is specified (Finnigan, 1979) and T is the observation time of one hour. Equation (16) was derived on the basis that, over a wheat canopy, discrete coherent gusts (known as Honomi) are seen to occur that deflect the plants, which then oscillate backwards and forwards until the motion is damped out. The relationship between the mean and gust velocities (equation 17) is valid for gusts above a canopy only. The method assumes that the canopy penetrating gusts can be specified at one metre above the canopy top. This must be regarded as a reasonable if significant assumption.

3.6. CALCULATION OF STEM FAILURE MOMENT

The stem failure moment, B_s, can be calculated from the standard formula of structural analysis for a cylinder.

$$\sigma = B_s a / I \quad (22)$$

where σ is the failure yield stress of the stem material, a is the external radius of the stem base and

I is the cross sectional second moment of area $\pi(a^4-(a-t)^4)/4$ where t is the wall thickness.

Thus

$$B_s = \frac{\sigma \pi a^3}{4}\left(1-\left(\frac{a-t}{a}\right)^4\right) \tag{23}$$

Values of a, σ and t need to be specified. Note that σ is the failure yield stress in tension. This is unlike the approach adopted by Graham (1983) who assumed that failure occurs due to compressive buckling of the stem. Such an analysis is not appropriate for a slender, thick walled column such as the internodal length of a wheat stem, although it could be argued that it might be appropriate for failure at the solid stem nodes. However a simple comparison of predicted failure strengths reveals that tensile failure is the critical condition.

3.7. CALCULATION OF ROOT FAILURE MOMENT

The root failure moment B_R is given by the method of Crook & Ennos (1993) who showed that

$$B_R = k_S s d^3 \tag{24}$$

where d is the root cone diameter and k_S is a constant. Crook & Ennos give a theoretical value

of 3.5 for this parameter (for an overturning disk on a soil surface), but their experiments give a value of close to 1.0. However results of the experiments reported in Griffin (1998; Fig. 2) where measured values of B_R (from mechanically loaded plants) were plotted against sd^3 suggest a much lower value of k_s of 0.43. The difference between these experimental results and the results of Crook & Ennos are probably due to the different methods of measuring root cone diameter - by careful excavation of the entire root/soil system in the case of Crook & Ennos, and by analysis of washed structural roots in Griffin (1998). The value k_s found by Griffin (1998) will be used because it was developed from a wider range of soil conditions than tested by Crook & Ennos (1993).

3.8. CALCULATION OF LODGING PROBABILITIES

For each pair of values of V and i, stem lodging is taken to occur if

$$B > B_s \qquad \text{and} \qquad NB < B_R \tag{25}$$

Root lodging is taken to occur if

$$B < B_s \text{ and} \qquad NB > B_R \tag{26}$$

where N is the average number of shoots per plant. Root and stem lodging together is taken to occur if

$$B > B_s \text{ and} \qquad NB > B_R \tag{27}$$

Thus by summing the number of lodging incidents predicted and dividing by 1000 the stem only, root only, stem and root combined and total lodging probabilities (p_S, p_R, p_{RS}, p_T) can be found for any one simulation of meteorological conditions. To relate the probability p_T to the total probability of lodging occurring during any one lodging period (P_T) (40 days centred on mid July) the following formulae (based on elementary statistical principles) are used.

$$P_T = \Sigma_{i\ -\ 1\ to\ 40}\ u_i \tag{28}$$

where

$$u_i = p_T\ (1 - \Sigma_{k=\ 1\ to\ I-1}\ u_k) \tag{29}$$

and $u_o = 0$. This represents the probability of lodging occurring in any one season. The return period for a lodging incident T_T is given by $1/P_T$.

4. Model results

In this section the model predictions for a set of standard parameters are considered in some detail. This is followed by the consideration of the results of a parametric analysis, that show the effects that variations in the different model parameters have on the predicted lodging risk. It should be noted that it is known that there are many interactions between the chosen parameters of the

model, but the parametric analysis helps by identifying those parameters having the largest effect on lodging risk.

The standard parameters of the lodging model are shown in Table 1, together with the range of these values normally found in the UK, that will be assumed in the parametric analysis. When the model is run with these standard parameters, each of the individual realisations of wind speed and rainfall lead to realisations of base bending moment (B) and root failure moment (B_R). Fig. 3 shows a number of histograms for the results of this case. Figures 3a and 3b show the probability distributions of daily maximum hourly mean wind speed and daily rainfall. These have the expected forms of the probability distributions given in equations (1) and (7). Fig. 3c shows a histogram of soil strength realisations. It can be seen that whilst this histogram has a main peak for soil strengths between 40 and 50kPa, there is a lower peak below 10kPa that represents the soil condition at field capacity. These values are associated with the high rainfall tail of Fig. 3b. Fig. 3d shows histograms of the base bending moment for all the shoots of a single plant (NB) and root failure moment (B_R). Only the lower tail of the latter histogram is shown - its main peak is actually at around 0.8 Nm, but a lower peak can be seen between 0.1 and 0.12 Nm due to the lower peak in soil strength values. It can be seen that these histograms overlap only to a small extent. It is for simultaneous realisations of NB and B_R in this overlap region that root lodging occurs (equation (26)). In fact for the standard conditions seven such realisations occur in 1000 realisations of wind speed and rainfall i.e. $p_R = 0.007$. Finally Fig. 3e shows the histogram of the base bending moment of a single shoot (B) together with the value of stem failure moment (B_S) which, being a function of stem parameters only, does not vary with wind and rainfall. It can be

seen that, for these standard conditions, B is always less than B_S so stem lodging does not occur and $p_S = 0$ (equation (26)). Similarly $p_{RS} = 0$ for these conditions and thus $p_T = 0.007$. Thus it can be seen that the extent to which lodging is predicted depends upon the relative positions of the value of B_S and the histograms of B, NB and B_R.

Now consider the results of the parametric analysis. The effect of varying each of the parameters defined in Table 1 over the ranges expected to occur in typical UK wheat crops will be demonstrated. The results of this analysis are shown in Table 2 which gives the combined stem and root lodging risk in a lodging season P_T for the maximum and minimum values of the individual parameters. Before discussing these results two points need to be made. Firstly, it must be noted that the value of risk varies in discrete steps - this is simply because the underlying probabilities for individual lodging realisations vary in discrete steps. For example the standard conditions shown in Table 1 give seven lodging events in a thousand realisations resulting in an overall probability for the lodging season of 0.245. If only six such events had been predicted, the probability would be 0.214 and if eight had been predicted the probability would have been 0.274. Secondly for variations in nearly all the parameters only root lodging is predicted and the variation of the lodging probability is monotonic with variations in the parameter. Thus in what follows the effect of variations in any of the parameters can mainly be judged simply by considering the lodging risk produced by the minimum and maximum values of the parameters i.e. from the results of Table 2. However where a very large variation in lodging risk is predicted over the parameter range, or where stem lodging occurs, or where the lodging risk variation is not monotonic, the

results will be considered in more detail than presented in Table 2.

Consider first the fixed model parameters. Table 2 shows the effect on lodging risk of variations in turbulence length scale, damping ratio, observation time, turbulence intensity and drag coefficient. None of these parameters are well specified in the literature. The range given is purely illustrative, but the results predict only root lodging for variation in all these parameters, as was the case with the standard values. Table 2 shows that the variations of lodging risk with variations in turbulence length scale, damping ratio and observation time are gratifyingly small, and thus the fact that their values are not well known is not too important. However the results are sensitive to variations in turbulence intensity and drag coefficient. These two parameters are not well specified, and these results suggest that further experimental data are needed to specify these parameters more precisely.

Now consider the site parameters. Table 2 show the effect of varying the hourly mean wind speed exceeded 50% of the time (V_{50}), the hourly mean wind speed exceeded 99% of the time (V_{99}), the daily rainfall exceeded 50% of the time (i_{50}) and the site altitude (h) respectively. Again only root lodging is predicted. As expected an increase in wind speed or site altitude increases lodging risk. Variations in V_{99} are most significant. Variations in i_{50} also produce a large change in the probabilities with an increase in root lodging risk as rainfall increases, as would be expected.

Now consider the soil parameters. Table 2 shows the effect of varying clay content, visual score for soil structure, soil water content at field capacity and soil water content at the permanent wilting point respectively. Only root lodging is predicted, which is not surprising since, as the standard values did not show stem lodging, it is not expected that variations in soil parameters will affect this. The effects of variation in clay content and visual score are very large indeed, with overall lodging risks varying between 0 and 1 as the parameters are varied. Variation in water content at permanent wilting point and field capacity are slightly smaller. An increase in clay content decreases lodging risk because the soil becomes stronger (Fig. 4a), an increase in the visual score increases lodging risk, because the soil becomes looser and weaker (Fig. 4b). An increase in water content at permanent wilting point increases lodging risk because less rainfall is required to wet the soil from its dry strong state to its wet weak state (Fig. 4c). Whilst the variations in risk are monotonic for these three parameters, variations in soil water content at field capacity have a more complex effect, with a peak in lodging risk at a value of 0.31 (Fig. 4d). This behaviour is due to the interactions between the terms containing water content at field capacity in equations (12) to (15). At this point however the artificiality of this parametric investigation should be noted - in reality all these soil properties will vary together. This will be discussed below.

Finally, the effect of varying the crop parameters is considered. Table 2 shows the effect of

variations in ear area, centre of gravity height, dry natural frequency, shoot number per plant, stem base radius, stem wall thickness, stem failure yield stress, root plate diameter and structural rooting depth respectively. Importantly, the variation of all these plant characters within typical UK wheat crops, apart from stem wall width, has a large effect on lodging risk. The effect of variation in ear area, centre of gravity height and natural frequency on lodging risk are in the expected directions. Lodging risk increases as ear area increases, centre of gravity height increases and as natural frequency decreases. As the shoot number per plant increases the risk of root lodging increases. With regard to the stem parameters, Fig. 5a shows the variation of the individual daily lodging risks p_S, p_R, p_{RS} and p_T for variations in stem radius and Fig. 5b shows the variation of combined stem and root lodging risk in one season P_T for this case. For this simulation it can be seen that as the radius falls below about 1.2mm the risk of stem lodging increases markedly. Similarly Figures 5c and 5d show the effect of variations in stem failure yield stress. Again, for this simulation, as this parameter falls below 20MPa stem lodging risk increases significantly. The effect of variations in stem wall width is minor. With regard to the root parameters Table 2 shows that a decrease in root plate diameter and structural rooting depth increases the risk of root lodging significantly. Once again the artificiality of this parametric investigation must be emphasised, since in practice large changes for individual crop characters whilst others remain unaltered are seldom observed. This is further considered in the discussion.

5. Discussion

In this section we will firstly discuss the overall nature of the model set out in the previous sections and its relationship to the actual process of lodging as observed in the field. An attempt will be made to compare the results of the model in a qualitative way with field experimental data. Secondly, the adequacy of the various assumptions made in the model will be considered. Finally, the implications of the results of the parametric analysis will be discussed.

Firstly then let us consider the nature of the model itself. The model was developed with a view to incorporating the major physical phenomena associated with lodging in a conceptual framework that could be easily and quickly implemented on PCs, and might ultimately prove useful in a practical situation. As such the prediction of lodging risk for a crop in any one year was seen to be of fundamental interest. However there are two implicit assumptions within the model. The first is that it assumes a constancy of crop parameters throughout the lodging season, yet it is known that these can vary significantly even during the period of highest lodging risk (Crook, Ennos & Sellers, 1994). The second is that it is implicit within the formulation that the lodging risk is predicted for a homogeneous area of crop during a particular lodging season. However it is known that crop and soil parameters and lodging risk can vary significantly throughout fields. For

example, lodging is found most often within the field headland, but is seldom found next to the tramlines used for field operations (Berry *et al.*, 1998). In addition, lodging very often seems to initiate at a vulnerable region, and surrounding plants lodge due to a 'domino' effect. Thus to properly validate the model, a very long term experiment would need to be carried out where a uniform crop is grown in uniform soil conditions over a large number of years. The proportion of years when lodging occurred would then represent the lodging probability as predicted by the model. Clearly even if it were possible to grow a uniform crop in uniform soil conditions, and to repeat this in succeeding years, such an experiment would not be possible within realistic resource limitations. The type of data that can readily be obtained however is information on the timing and proportion of crop area lodged for different crop and soil types. Thus to confirm the adequacy or otherwise of the modelling approach it would seem that there are two possible courses of action. Firstly the model could be extended to take into account spatial non-uniformity of crop and soil, and variations in these parameters through the lodging season. Whilst this would certainly be possible, and would indeed have some merit as a fundamental research tool for the investigation of the lodging phenomenon, it would significantly increase the complexity of the model in computational terms and make its repeated use difficult and computationally very expensive. The other approach, the one followed here, is to view the model results as giving an indication of the susceptibility of a crop to lodging. As such its results can be compared directly with measured indicators of crop susceptibility to lodging such as percentage area lodged in a particular season.

The procedure followed to assess the adequacy of the model was as follows. Firstly the data from

the experiments reported in Berry *et al.* (1998) and Griffin (1998) comparing the effect of different agronomic treatments on the parameters that affect lodging risk, and lodging itself, was analysed. For each experimental plot a graph of percentage lodged area against time was produced and the area under the curve found. This gives some indication of the susceptibility of the crop to lodging - significant early season lodging will occur for the susceptible plots, and thus the area under the lodging curve will be high, whilst for those less susceptible plots only late season lodging will occur with a smaller proportion of area lodged, and thus the area under the lodging curve will be small. The data for the individual plots was then ranked, i.e. the plot with the smallest area under the lodging curve was given a value of one, the next a value of two and so on. The model was then run for the soil and crop parameters measured in July for each plot, and lodging risks calculated. The plots were then given a rank in terms of predicted lodging risk in a similar way. Some plots were predicted to have identical lodging risks and these plots were given equal ranks. The two sets of rankings were then plotted against each other, as shown in Fig. 6. The results are encouraging. There were 38 plots where no lodging was observed or predicted by the model (shown as one point near the origin of the graph). There were a further 21 plots where large amounts of lodging occurred which was predicted by the model, shown by the points in the upper right of the graph. In four plots lodging was predicted where none occurred (the points near the y axis of the graph) and in nine plots lodging was observed but not predicted (the points near the x axis of the graph). The model thus correctly predicted lodging in 21of the 30 lodged crops and nil lodging for 38 of the 42 standing crops, i.e. for 82% of the experimental plots the model can be seen to be predicting lodging susceptibility quite well. These results give some confidence in the applicability of the model.

Now let us consider the various assumptions made in the model. Firstly consider the assumptions made about the meteorological conditions. It was assumed that the parameters of relevance to the lodging process were the daily rainfall and the maximum wind gust that could be expected to occur in any one day. The probability distributions for obtaining realisations of these parameters are reasonably well founded and reliable. However, in reality it is likely that the wind and rain probability distributions will not be independent as assumed in the model, but linked in some way. The model does not take this into account because of a lack of readily available data on linkage. An analysis of suitable met station measurements could provide the necessary information if sufficient resources were available to carry out such a study in the future. It was further assumed that the nature of the wind above a wheat canopy is such that occasional strong gusts penetrate down into the canopy, and these are the ones associated with the lodging process. In broad terms this is in agreement with published data, but a major assumption made here is that the strength of these gusts can be estimated from the wind characteristics about one metre above the top of the canopy. This assumption must be regarded as fairly arbitrary.

Now consider the nature of the dynamic model used to predict the stem base bending moment. This is based on the work of Baker (1995) and its application to isolated and forest trees suggests it is a reasonable approximation to reality. Effectively it assumes a two mass system - one mass representing the ear, and the other representing the root ball, connected by a weightless elastic

stem, and is relatively simple to implement. It suggests that the natural frequency is a parameter of major importance in determining the stem base bending moment. The major weakness of this aspect of the model is the rather arbitrary correction of natural frequency to allow for root loosening effects when the soil is weakened by moisture i.e. the value k_4. More experimental data is required here.

The root component of the model is based on the work of Crook & Ennos (1993) and represents a straightforward way of relating root failure moment to root plate diameter and the shear strength of clay soils, that is dimensionally correct and theoretically reasonable. There is some uncertainty in the value of the constant of proportionality within the model (k_5), and more work is needed to determine this constant for a variety of clay soil types. Further investigations must also discover how appropriate the model of root lodging is for soils containing no clay, such as sands. The strength of these soil types result more from intergranular friction than from the cohesive forces found in clay soils. This may mean that the mechanism by which plants root lodge in soils containing little or no clay is quite different.

The soil component requires the most modification of the various aspects of the model. Whilst being set in a theoretically consistent format, its precise nature is very dependent upon experimental work carried out on only one soil type, and it is only strictly applicable to soils with a clay content greater than 0.15g/g. More experimental information for different soil types might

help to better define this aspect of the model, although determination of soil strength for surface layers of different agricultural soil types is not trivial.

In the implementation of the model a number of parameter values are assumed (see the fixed parameter list of Table 1). The results from the model suggest that whilst the predicted lodging risks are not particularly sensitive to some of these parameters (turbulence length scale, damping ratio, observation time) it is reasonably sensitive to others (turbulence intensity, drag coefficient). Again more experimental data is needed to better define the range of values for these parameters.

The model assumptions having been considered, let us now consider the implications of the results of the parametric analysis of the last section. From the results of the parametric analysis shown in Table 2 and Figures 3 to 5 the following main points emerge.

a) The occurrence of root, stem or combined root and stem lodging depends upon the relative magnitudes of a number of variables - it is overly simplistic to state that lodging is due to one or other of the mechanisms, since, given suitable circumstances both may occur. Nonetheless root lodging was the most frequently predicted form of lodging, as has been found by previous authors (Pinthus, 1973, Graham, 1983, Easson *et al.*, 1993).

b) Variation in UK wheat crop characteristics influence lodging risk as much, or more, than the weather at the time of lodging. The state of a wheat crop can be manipulated by different cropping practices, thus indicating that lodging risk may be effectively controlled despite the unpredictable influence of weather.

c) It should be noted that soil water content at field capacity and permanent wilting point are strongly influenced by clay content and soil structure. For example, a soil with a high clay content is inherently strong and would be expected to decrease root lodging risk. However, this type of soil also has a high water content at field capacity (Bowell, 1994) which will reduce its strength in the wet state. This study indicates that wheat crops grown on soils containing a large proportion of clay are less lodging prone than crops grown on lighter soils. However, more precise information about the relationship between the clay and water contents of different soils is required to provide firm conclusions about this. The relationship between soil characteristics and lodging risk is further complicated by the effects of soil on the aerial components of the crop. Crops on light soils are more prone to water and nutrient deficiencies, with the consequent reductions in above ground growth. This is likely to manifest itself in, for example, fewer shoots per plant, shorter stems (lower centre of gravity) and possibly reduced ear area. All of these characters will result in a smaller base bending moment being exerted on the root/soil system and smaller lodging risk.

d) The importance of variation in certain crop characters on lodging risk is apparent. However, the results of the parametric analysis for the effects of individual crop characters on lodging risk must be treated with caution because only occasionally will individual characters change whilst others remain unaltered. More commonly, crop characters do not vary independently. Berry *et al.* (1998) observed that reduction of seed rate caused an increased shoot number per plant but a proportionally greater increase in root plate diameter and root failure moment. Therefore, in this case an increase in shoot number was associated with a reduction in root lodging risk. Strong positive correlations have been observed for root plate diameter with structural rooting depth and stem base radius with stem wall width. Height at centre of gravity has been negatively correlated with natural frequency. It is probable that other correlations which are more complex also exist. In order to carry out a more realistic parametric analysis, related plant characters need to be identified and varied together. This may be carried out most effectively by investigating the effects of husbandry practice on the lodging associated plant characters and lodging risk.

6. Concluding remarks

From the preceding sections it can be seen that the lodging model as developed is a useful tool to help understand the lodging process, and its predictions for crop susceptibility to lodging are in broad agreement with lodging experienced in field experiments. The model has proved to be particularly useful for the identification of crop and soil parameters that are of most significance

to the lodging process. These include soil clay content, soil visual score, root plate diameter, shoot number per plant, natural frequency, stem radius and stem failure yield stress. This suggests that to reduce lodging risk energies should be directed towards making modifications to these parameters wherever possible.

However the model has certain limitations, some of them severe. There are a number of parameters that have not been fully considered - in particular ear drag coefficient, turbulence intensity and the coefficients of proportionality k_4 and k_5. Also the nature of wind gust above crop canopies is not well specified, and the various formulae used to calculate soil strength are to a large extent based on empirical data. More fundamental experimental work is required in these areas to optimise the model.

The model itself could also be usefully extended to take account of spatial non-uniformity in the crop and variations in the crop parameters through the lodging season. Whilst such a model would be necessarily complex and computationally expensive, it would nonetheless be an extremely useful research tool to further help in understanding and controlling the lodging process.

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Notation

a	stem base radius
A	ear area
B	wind induced base bending moment
B_R	root failure moment
B_S	stem failure moment
c	clay content
c_R	reference value of c
C_D	drag coefficient
d	root plate diameter
f	water content at field capacity (by weight)
g	acceleration due to gravity
g_v	velocity gust factor
h	site altitude
i	daily mean rainfall
i_{50}	daily mean rainfall exceeded 50% of the time
I	second moment of area of stem base
J_1	function in equation (20)
J_2	function in equation (21)
k_1	constant in wind Weibul distribution
k_2	constant in wind Weibul distribution
k_3	constant in rainfall distribution
k_4	constant in equation (11)
k_5	constant in equation (24)
l	structural rooting depth
L	function in equation (18)
${}^{x}L_V$	turbulence length scale
n	natural frequency
n_D	natural frequency in dry soil conditions
n_W	natural frequency in wet soil conditions
N	number of shoots per plant
p_r	probability of daily mean rainfall
P_r	exceeding i
p_R	probability of root lodging
p_{RS}	probability of stem and root lodging
p_S	probability of stem lodging
p_T	total lodging probability
p_W	probability of daily maximum hourly mean wind speeds exceeding V
P_T	lodging probability in one season
s	soil shear strength
s_D	s at permanent wilting point
s_W	s at field capacity
t	stem wall thickness
T	observation time
T_T	lodging return period
u_i	term in equation (28)
v	visual source
v_R	reference value of v
V	daily maximum hourly mean wind speed
V_g	gust wind speed
V_{50}	corrected value of V_{50}'
V_{99}	corrected value of V_{99}'
V_{50}'	hourly mean wind speed exceeded 50% of time
V_{99}'	hourly mean wind speed exceeded 1% of time
X	centre of gravity height of shoot
w	water content at permanent wilting point (by weight)
z_O	surface roughness length
δ	plant damping ratio
ρ	density of air
ρ_S	density of soil
ρ_W	density of water
σ	stem failure yield stress
σ_V	wind turbulence

Captions for Figures

Fig. 1 Outline of method for assessing lodging risk.

Fig. 2 The product of soil shear strength (s) and root plate diameter cubed (d^3) plotted against root failure moment (B_R).

Fig. 3 Daily probability distributions for the standard case (a) Maximum hourly mean wind speed probability distribution, (b) Rainfall probability distribution, (c) Soil strength probability distribution, (d) Shoot base bending moment x number of shoots per plant (hatched bars) and anchorage failure moment (open bars) probability distributions, (e) Shoot base bending moment (hatched bars) and stem failure moment (open bar) probability distributions.

Fig. 4 Variations in seasonal root lodging risk for variations in soil conditions, (a) Soil clay content, (b) Visual score of soil structure, (c) Soil water content at permanent wilting point, (d) Soil water content at field capacity.

Fig. 5 Variation of lodging risk with variation in stem parameters, (a) Root (■), stem (•) and root + stem (○) daily lodging risks with variation in stem radius, (b) Combined risk of stem and root lodging in one season due to variation in stem radius, (c) Root (■), stem (•) and root + stem (○) daily lodging risks with variation in stem failure yield stress, (d) Combined risk of stem and root lodging in one season with variation in stem failure yield stress.

Fig. 6 Experimental and model predicted rankings of lodging susceptibility of wheat crops managed with different agronomic inputs.

Table 1 Ranges of the standard parameters expected in the UK.

Parameter	Notation	Standard value	Range of values for UK	Source
Fixed model parameters				
Turbulence length scale (m)	${}^{x}L_{v}$	1.25	1.0 to 1.5	F79
Damping ratio	δ	0.05	0.03 to 0.07	A
Observation time (s)	T	3600	1800 to 5400	A
Turbulence intensity	σ_V/V	0.50	0.4 to 0.6	F79
Ear drag coefficient	C_D	0.3	0.2 to 0.4	G83
Meteorological and site parameters				
Hourly wind speed exceeded 50% of time (m/s)	V_{50}	4	3 to 5	C85
Hourly wind speed exceeded 99% of time (m/s)	V_{99}	10	8 to 12	C85
Daily rainfall exceeded 50% of time (mm)	i_{50}	2	1 to 3	S83
Site altitude (m)	h	50	0 to 200	A
Soil parameters				
Clay content (g/g)	c	0.25	0.2 to 0.4	B94
Visual score	v	5	2 to 8	M82
Water content at permanent wilting point (g/g)	w	0.15	0.1 to 0.2	B94
Water content at field capacity (g/g)	f	0.27	0.2 to 0.35	B94
Crop parameters				
Ear area (m^2)	A	0.001	0.0006 to 0.0012	B98
Centre of gravity height (m)	X	0.5	0.2 to 0.8	C94
Dry natural frequency (Hz)	n	1	0.5 to 1.5	G83
Number of shoots per plant	N	3	1 to 9	E93
Stem base radius (mm)	a	1.5	1 to 3	G83
Stem wall thickness (mm)	t	0.5	0.3 to 0.75	G83
Stem failure stress (MPa)	σ	40	15 to 50	G83
Root plate diameter (mm)	d	35	10 to 80	C93
Rooting depth (mm)	l	35	15 to 60	B98

Key to sources: Author estimates based on A author estimate, B98 experiments reported in Berry *et al.* (1998), B94 Bowell (1994), C85 Cook (1985), C93 Crook and Ennos (1993), C94 Crook *et al.* (1994), E93 Easson *et al.* (1993), F79 Finnigan (1979), G83 Graham (1983), M82 MAFF (1982), S83 Shaw (1983).

Table 2 Parametric analysis

Parameter	Seasonal lodging risk (P_T) at minimum parameter value	Seasonal lodging risk (P_T) at maximum parameter value
Fixed model parameters		
Turbulence length scale (m)	0.214	0.303
Damping ratio	0.303	0.245
Observation time (s)	0.214	0.274
Turbulence intensity	0.113	0.636
Ear drag coefficient	0.004	0.691
Meteorological and site parameters		
Hourly wind speed exceeded 50% of time (m/s)	0.213	0.589
Hourly wind speed exceeded 99% of time (m/s)	0	0.621
Daily rainfall exceeded 50% of time (mm)	0.077	0.407
Site altitude (m)	0.213	0.636
Soil parameters		
Clay content (g/g)	1	0
Visual score	0	1
Water content at permanent wilting point (g/g)	0.181	0.572
Water content at field capacity (g/g)	0	0.716
Crop parameters		
Ear area (m^2)	0	0.605
Centre of gravity height (m)	0.039	0.704
Dry natural frequency (Hz)	0.934	0.113
Number of shoots per plant	0	1
Stem base radius (mm)	0.996	0.245
Stem wall thickness (mm)	0.274	0.245
Stem failure stress (MPa)	0.979	0.245
Root plate diameter (mm)	1	0
Rooting depth (mm)	0.636	0.148

FIG. 1

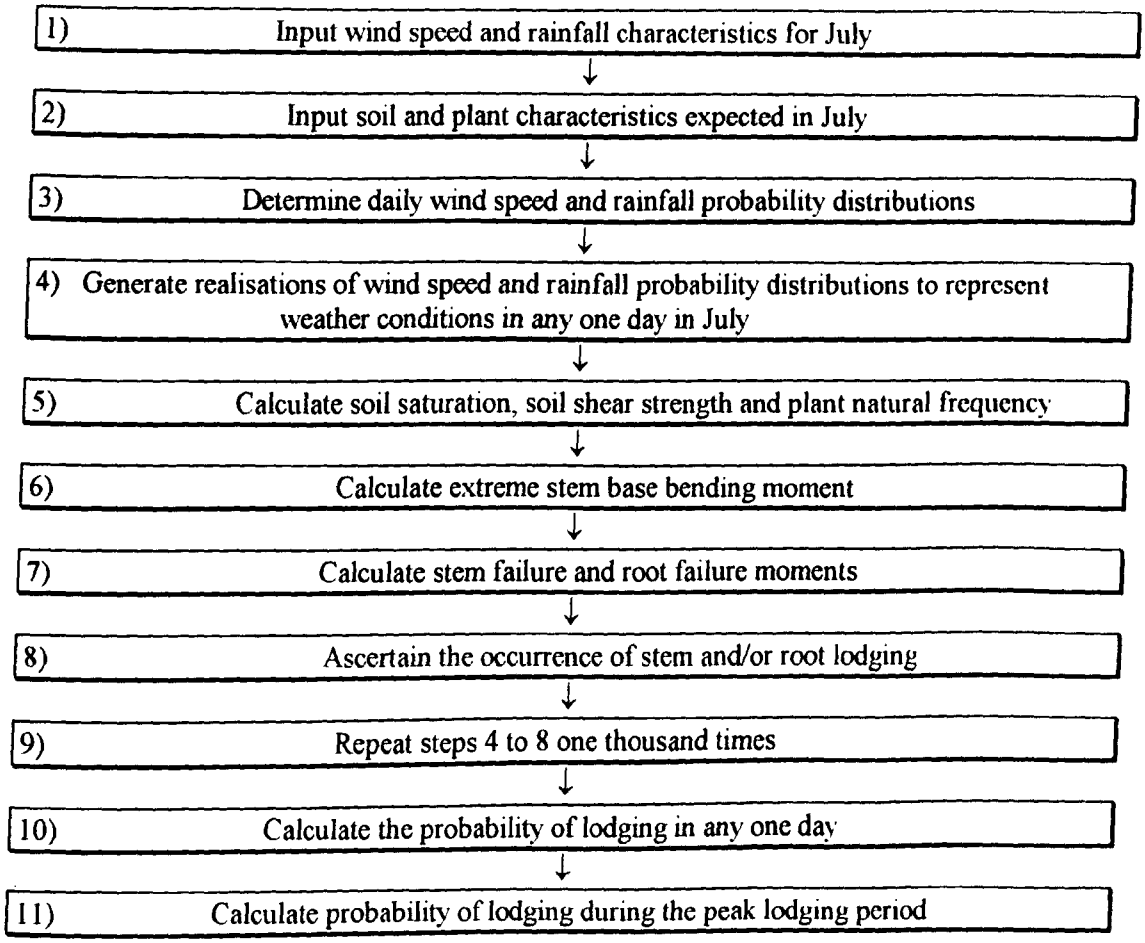

1) Input wind speed and rainfall characteristics for July
2) Input soil and plant characteristics expected in July
3) Determine daily wind speed and rainfall probability distributions
4) Generate realisations of wind speed and rainfall probability distributions to represent weather conditions in any one day in July
5) Calculate soil saturation, soil shear strength and plant natural frequency
6) Calculate extreme stem base bending moment
7) Calculate stem failure and root failure moments
8) Ascertain the occurrence of stem and/or root lodging
9) Repeat steps 4 to 8 one thousand times
10) Calculate the probability of lodging in any one day
11) Calculate probability of lodging during the peak lodging period

FIG 2

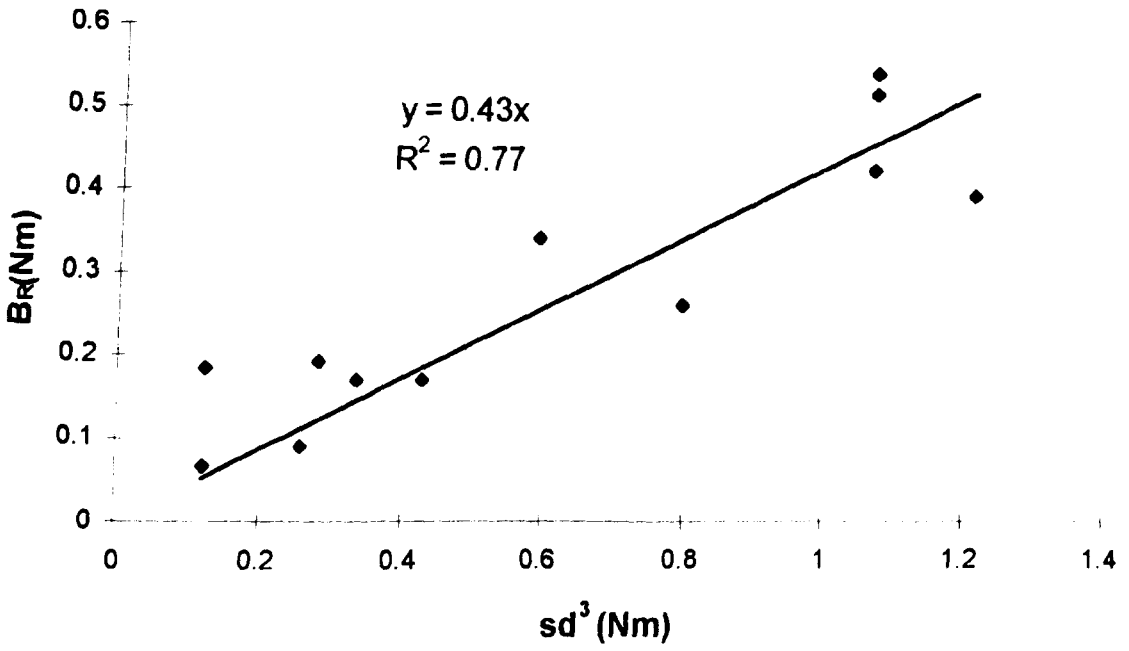
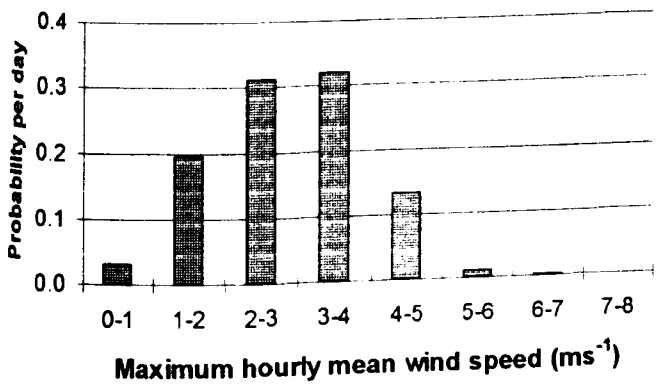
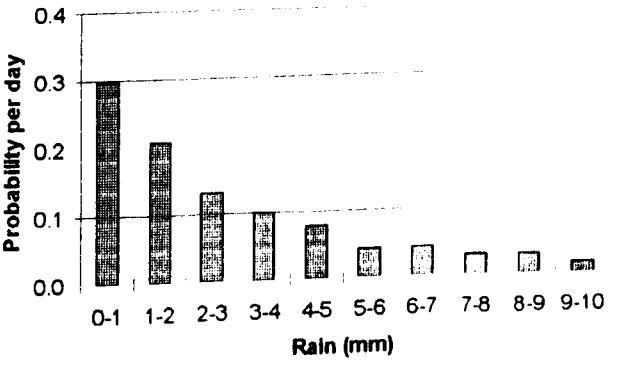


FIG.3

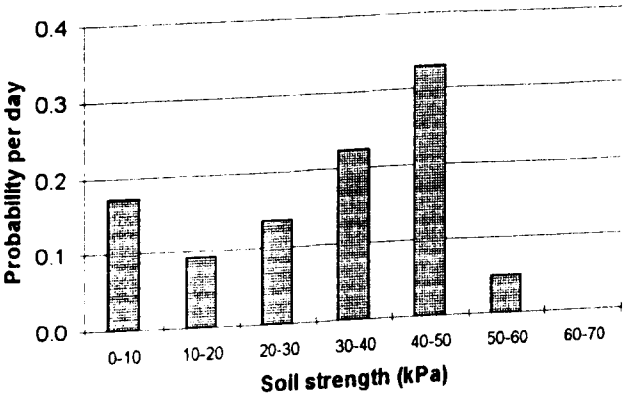
(a)


Probability per day
0.4
0.3
0.2
0.1
0.0
0-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
Maximum hourly mean wind speed (ms-1)

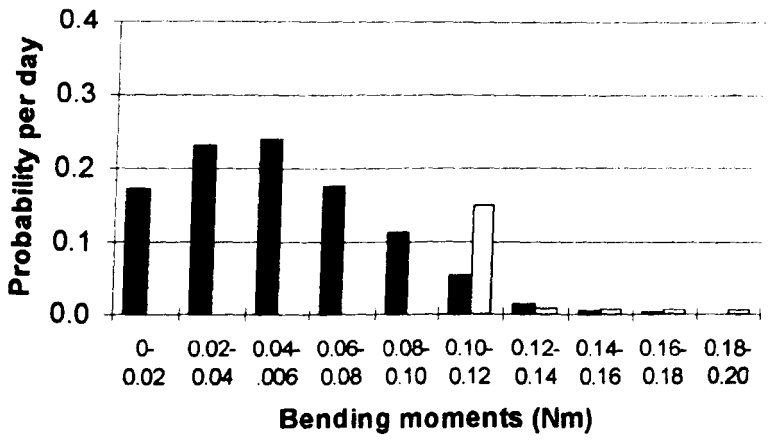
(b)


Probability per day
0.4
0.3
0.2
0.1
0.0
0-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-10
Rain (mm)

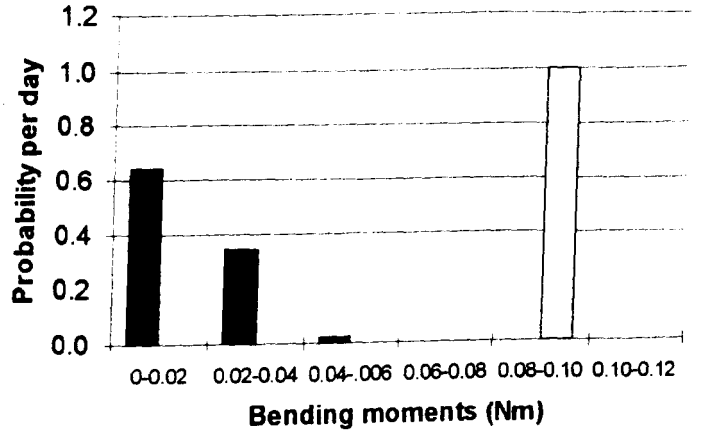
(c)


Probability per day
0.4
0.3
0.2
0.1
0.0
0-10
10-20
20-30
30-40
40-50
50-60
60-70
Soil strength (kPa)

(d)

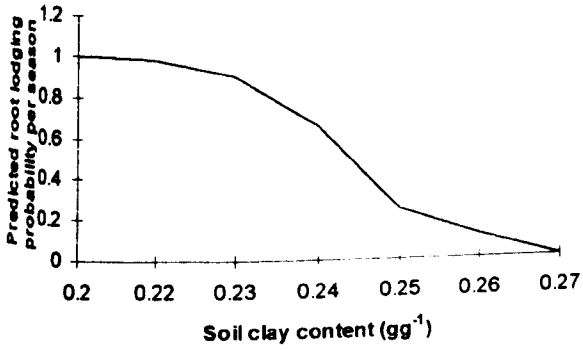

0.4
0.3
0.2
0.1
0.0
Probability per day
0-0.02
0.02-0.04
0.04-.006
0.06-0.08
0.08-0.10
0.10-0.12
0.12-0.14
0.14-0.16
0.16-0.18
0.18-0.20
Bending moments (Nm)

(e)

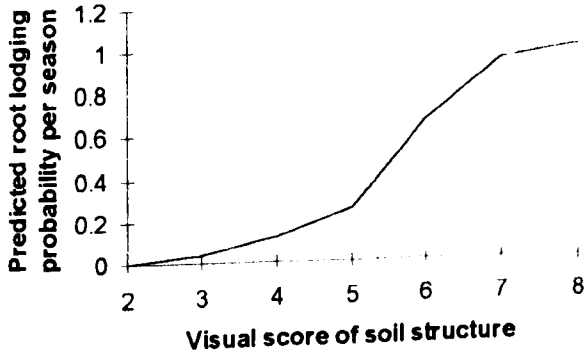

1.2
1.0
0.8
0.6
0.4
0.2
0.0
Probability per day
0-0.02
0.02-0.04
0.04-.006
0.06-0.08
0.08-0.10
0.10-0.12
Bending moments (Nm)

FIG

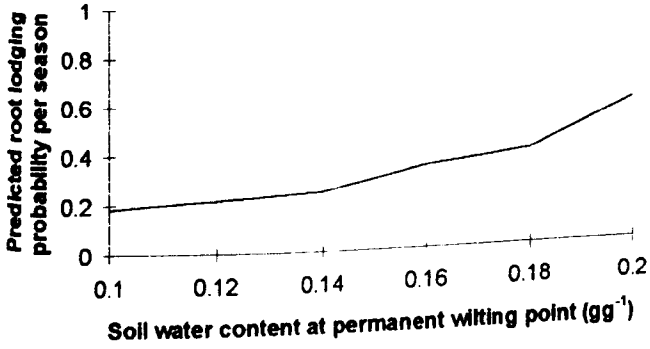
(a)


Predicted root lodging probability per season
1.2
1
0.8
0.6
0.4
0.2
0
0.2
0.22
0.23
0.24
0.25
0.26
0.27
Soil clay content (gg-1)

(b)


Predicted root lodging probability per season
1.2
1
0.8
0.6
0.4
0.2
0
2
3
4
5
6
7
8
Visual score of soil structure

(c)


Predicted root lodging probability per season
1
0.8
0.6
0.4
0.2
0
0.1
0.12
0.14
0.16
0.18
0.2
Soil water content at permanent wilting point (gg-1)

(d)

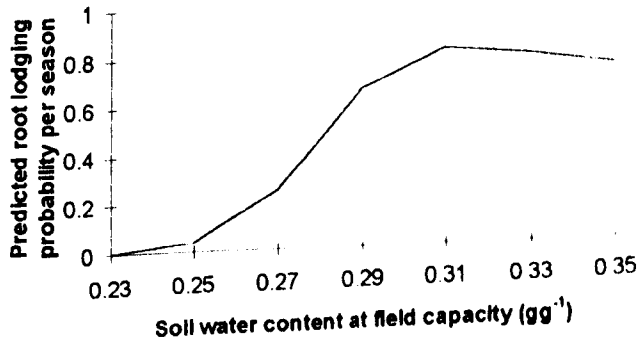
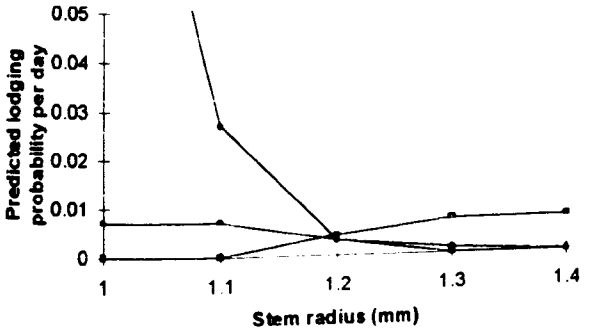
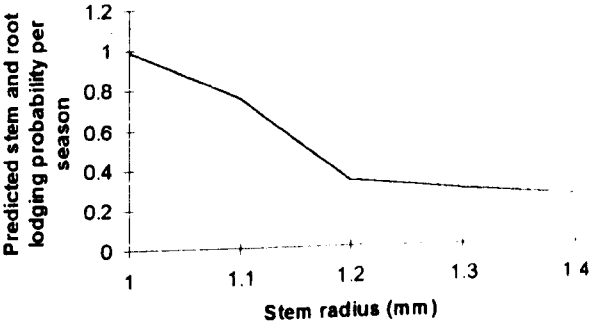

Predicted root lodging probability per season
1
0.8
0.6
0.4
0.2
0
0.23
0.25
0.27
0.29
0.31
0.33
0.35
Soil water content at field capacity (gg-1)

FIG 5.

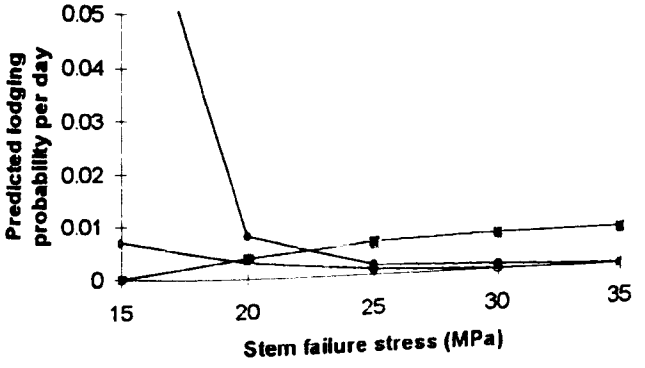
(a)


Predicted lodging probability per day
0.05
0.04
0.03
0.02
0.01
0
1
1.1
1.2
1.3
1.4
Stem radius (mm)

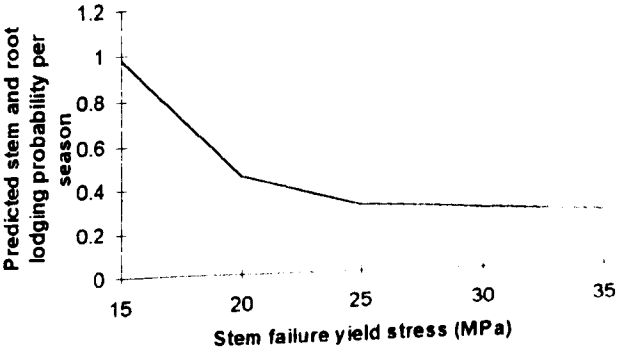
(b)

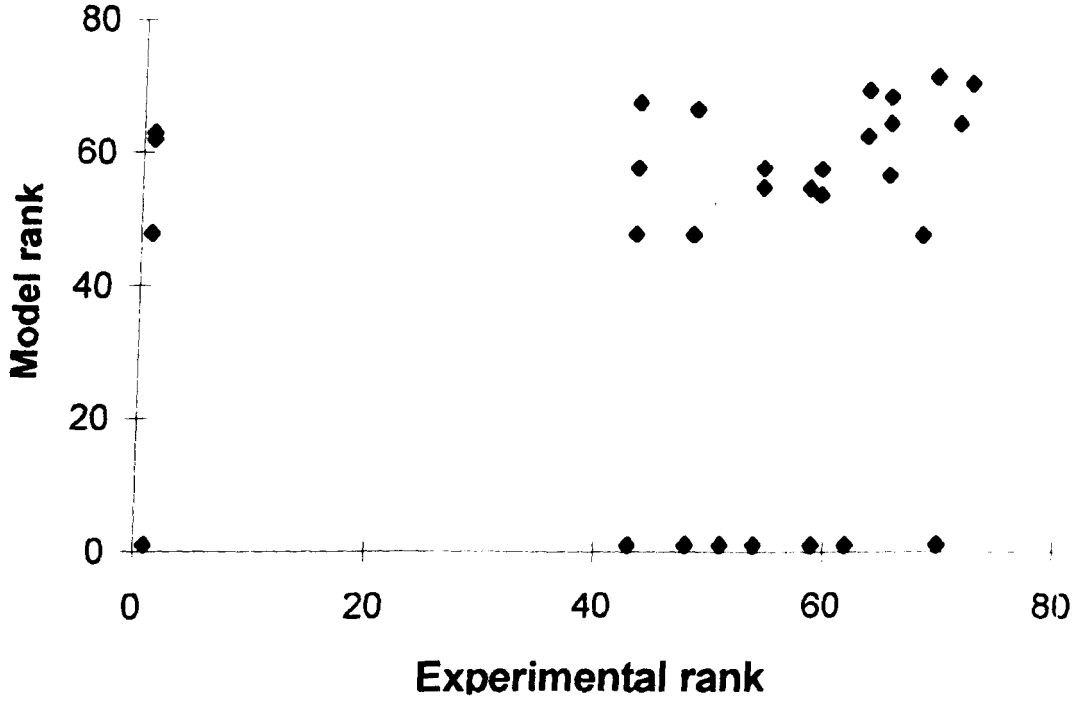

Predicted stem and root lodging probability per season
1.2
1
0.8
0.6
0.4
0.2
0
1
1.1
1.2
1.3
1 4
Stem radius (mm)

(c)


Predicted lodging probability per day
0.05
0.04
0.03
0.02
0.01
0
15
20
25
30
35
Stem failure stress (MPa)

(d)


Predicted stem and root lodging probability per season
1.2
1
0.8
0.6
0.4
0.2
0
15
20
25
30
35
Stem failure yield stress (MPa)


80
60
40
20
0
Model rank
0
20
40
60
80
Experimental rank

APPENDIX 2

HGCA INTERGRATED LODGING, LINK-N AND DEVELOPMENT TRIAL

BELMONT 1994-1995 WINTER WHEAT CV. MERCIA

PLOT DIMENSIONS : 18m x 4m PLOTS, WITH 12m INTERNAL HEADLANDS

| | | |

JUBILEE 95-96 WINTER WHEAT CV MERCIA

PLOT DIMENSION 24M X 3M

| | | |

APPENDIX 3

PLANT ASSESSMENT SCHEDULES

Appendix 3.1 MT95

Growth stages at which plants were sampled are shown in Table 3a and the measurements which were taken at each of these growth stages are shown in Table 3b. At each growth stage the measurements described in Table 3b were taken for different treatments. The treatments which were investigated at each growth stage are described below.

At GS 30 and GS 31 measurements were taken on the sowing date, seed rate, residual nitrogen and nil lodging control treatments. At GS 33 and GS 39 measurements were taken on the same treatments as for the previous two growth stages, and for the 5C Cycocel lodging control treatments.

The weekly assessments began after GS 39 and assessed two sets of treatments; the early sown, high seed rate, high residual nitrogen and 5C Cycocel with Terpal treatment combination (collectively known as 'high lodging risk with PGR') and the late sown, low seed rate, low residual nitrogen and 5C Cycocel with Terpal treatment combination (collectively known as 'low lodging risk with PGR').

At GS 59 and GS 72 measurements were taken on the early sown, high seed rate, high residual nitrogen and Canopy Management treatment combination, in addition to the treatment combinations assessed weekly. At GS 69 measurements were taken on all treatments. At harvest (GS 90) the measurements described in Table 3b were taken for all treatments.

Table 3a Sampling dates

GROWTH STAGE	EARLY SOWING	LATE SOWING
GS 30	23/2/95	3/4/95
GS 31	22/3/95	10/4/95
GS 33	27/4/95	3/5/95
GS 39	12/5/95	18/5
GS 59	5/6/95	5/6/95
GS 69	26/6/95	26/6/95
GS 72	3/7/95	3/7/95
GS 90 (HARVEST)	9/8/95	9/8/95

Table 3b Plant measurements

MEASUREMENT	GS 30	31	33	39	WK LY	59	69	72	Har-vest
GROWTH ANALYSIS									
SOIL MINERAL N kg/ha	✓								
DRY PLANT N %	✓	✓							
PLANT NUMBER/m^2	✓	✓							
SHOOT/EAR NUMBER/m^2	✓	✓	✓	✓		✓		✓	✓
TOTAL FWT, DWT t/ha & GAI	✓	✓	✓	✓		✓		✓	
LEAF FWT, DWT t/ha & LAI	✓	✓	✓	✓		✓		✓	
STEM FWT, DWT t/ha & SAI	✓	✓	✓	✓		✓		✓	
EAR FWT, DWT t/ha & EAI						✓		✓	
10 PLANT SAMPLES									
CROWN DEPTH/cm	✓	✓	✓	✓		✓		✓	
CROWN WIDTH/cm				✓		✓		✓	
PLANT DIAM. AT SURFACE/mm			✓	✓		✓		✓	
ROOT NUMBER per PLANT	✓	✓	✓	✓	✓	✓	✓	✓	
LENGTH OF RIGID ROOTS/mm	✓	✓	✓	✓		✓		✓	
MAX.ROOT CONE DIAM. /mm	✓	✓	✓	✓	✓	✓	✓	✓	
MIN. ROOT CONE DIAM/mm				✓	✓	✓	✓	✓	
MAX ROOT CONE ANGLE	✓	✓	✓	✓	✓	✓		✓	
MIN ROOT CONE ANGLE				✓	✓	✓		✓	
ANCHORAGE RESISTANCE/Nm					✓				✓
SHOOT NUMBER per PLANT	✓	✓	✓	✓	✓	✓	✓	✓	
HEIGHT/cm		✓	✓	✓	✓	✓	✓	✓	
CENTRE OF GRAVITY (PLANT)/cm				✓	✓	✓		✓	
CENTRE OF GRAVITY (M.S)/cm				✓	✓	✓	✓	✓	
NATURAL FREQUENCY					✓				✓
PLANT FRESH WEIGHT/g					✓	✓		✓	
AVERAGE EAR AREA/ cm^2					✓	✓		✓	
AVERAGE EAR FRESH WEIGHT/g					✓			✓	
INTERNODES BASAL, 1 & 2									
LENGTH/mm			✓	✓		✓		✓	✓
DIAMETER/mm			✓	✓		✓		✓	✓
WALL WIDTH/mm				✓				✓	
WEIGHT/g				✓				✓	
BENDING MOMENT/N				✓		✓		✓	

Appendix 3.2 MT96

Growth stages at which plants were sampled are shown in Table 3c. The measurements which were taken at each of these growth stages are shown in Table 3d. December measurements were taken on the first sowing date, seed rate, residual nitrogen and nil lodging control treatments. In January, February and March and at GS 30 and GS 31 measurements were taken on the sowing date, seed rate, residual nitrogen and nil lodging control treatments. At GS 33 and GS 39 measurements were taken on the same treatments as for the previous two growth stages, and for the 5C Cycocel lodging control treatment. At GS 72 measurements were taken for all treatments. At GS 85 measurements were taken for the sowing date, seed rate, residual nitrogen and nil lodging control treatments, together with the four lodging control treatments of the early sown, high seed rate and high residual nitrogen treatment combination. At harvest measurements were taken on all treatments.

Table 3c Sampling dates

GROWTH STAGE	EARLY SOWING	LATE SOWING
GS 21 - 27	11/12/95	-
GS 21 - 27	15/1/96	15/1/96
GS 21 - 27	14/2/96	14/2/96
GS 22 - 26	-	18/3/96
GS 30	18/3/96	22/4/96
GS 31	2/4/96	29/4/96
GS 33	26/4/96	14/5/96
GS 39	24/5/96	31/5/96
GS 72	1/7/96	4/7/96
GS 85	31/7/96	31/7/96
GS 90 (HARVEST)	19/8/96	19/8/96

Table 3d Plant measurements

MEASUREMENT	Dec	Jan	Feb	Mar	GS 30	31	33	39	72	Har-vest
GROWTH ANALYSIS										
SOIL MINERAL N kg/ha	✓	✓	✓	✓	✓					
DRY PLANT N %	✓	✓	✓	✓	✓	✓				
PLANT NUMBER/m^2	✓	✓	✓	✓	✓	✓				
SHOOT NUMBER/m^2	✓	✓	✓	✓	✓	✓	✓	✓		
TOTAL FWT, DWT t/ha, GAI	✓	✓	✓	✓	✓	✓	✓	✓		
LEAF FWT, DWT t/ha, LAI	✓	✓	✓	✓	✓	✓	✓	✓		
STEM FWT, DWT t/ha, SAI	✓	✓	✓	✓	✓	✓	✓	✓		
10 PLANT SAMPLES										
CROWN DEPTH/mm					✓	✓	✓	✓	✓	✓
ROOT NUMBER per PLANT					✓	✓	✓	✓	✓	✓
MAX.ROOT CONE DIAM. /cm					✓	✓	✓	✓	✓	✓
MIN. ROOT CONE DIAM/cm					✓	✓	✓	✓	✓	✓
MAX ROOT CONE LENGTH/mm					✓	✓	✓	✓	✓	✓
MIN ROOT CONE LENGTH/mm					✓	✓	✓	✓	✓	✓
SHOOT NUMBER per PLANT					✓	✓	✓	✓	✓	✓
HEIGHT/cm					✓	✓	✓	✓	✓	✓
CENTRE OF GRAVITY (MS)/cm								✓	✓	✓
PLANT FRESH WEIGHT/g									✓	
NATURAL FREQUENCY									✓	✓
AVERAGE EAR AREA/ cm^2									✓	✓
INTERNODES BASAL, 1 & 2										
LENGTH/mm							✓	✓	✓	✓
DIAMETER/mm							✓	✓	✓	✓
WALL WIDTH/mm							✓	✓	✓	✓
BENDING MOMENT/N							✓	✓	✓	✓

Additional measurements
Height and ceptometer measurements were taken weekly from GS 31 until GS 39 on the sowing date, seed rate and residual nitrogen treatments combinations.

At harvest (GS 90) yield (t ha^{-1}), thousand grain weight (g), specific weight (g) moisture content (%), harvest index and ear number m^{-2} were measured for all treatments.

Appendix 3.3 VT95

The variety experiment was sampled at GS 31, GS 39 and GS 65 + 75°Cd^{-1}. The measurements which were taken at each of these growth stages are shown in Table 3e. A core subset of five varieties were measured at all three sampling stages. These varieties included little Joss, Beaver, Mercia which represented the bench mark variety as it was used in the main experiments, Riband and Hereward.

In addition to the core subset varieties, measurements were taken on as many other varieties as time allowed. Measurements were first taken at GS 31 on the core subset of varieties together with Ami, Apollo, Avalon, Avital, Brigadier, Norman, Rialto, Scipion, Soissons and Squareheads Master. At GS 39 measurements were taken on core subset varieties only. At GS 65 + 75°Cd^{-1} measurements were taken for the core subset plus Ami, Avalon, Apollo, Avital, Buster, Cadenza, Florin, Hunter, Longbow, Maris huntsman, Mercia Norman, Rialto, Scipion, Soissons and Spark. Stem strength measurements were only recorded on the core subset plus Apollo, Buster and Cadenza. Height and natural frequency were measured on all the varieties just before harvest.

Table 3e Plant assessment schedule

MEASUREMENT	GS 31	GS 39	GS 65	HARVEST
10 PLANT SAMPLES				
CROWN DEPTH/mm	✓	✓	✓	
CROWN WIDTH/mm		✓		
PLANT DIAM. AT SOIL SURFACE/mm	✓	✓	✓	
ROOT NUMBER per PLANT	✓	✓	✓	
RIGID LENGTH OF ROOTS/mm	✓	✓	✓	
MAX.ROOT CONE DIAM. /mm	✓	✓	✓	
MIN. ROOT CONE DIAM/mm		✓	✓	
MAX ROOT CONE ANGLE	✓	✓	✓	
MIN ROOT CONE ANGLE		✓	✓	
SHOOT NUMBER per PLANT	✓	✓	✓	
HEIGHT/cm	✓	✓	✓	✓
CENTRE OF GRAVITY (PLANT)/cm		✓	✓	
CENTRE OF GRAVITY (MS)/cm		✓	✓	
EAR AREA/ cm^2			✓	
EAR FWT/g			✓	
NATURAL FREQUENCY				✓
INTERNODES BASAL, 1 & 2				
LENGTH/mm		✓	✓	
DIAMETER/mm		✓	✓	
WALL WIDTH/mm		✓	✓	
WEIGHT/g		✓	✓	
BENDING MOMENT/N		✓	✓	

APPENDIX 4

MEASUREMENTS SCHEDULE FOR LODGED PLOTS

Scoring plot area :

- 4 x 10m^2 area left unsampled, for lodging to be assessed.
- Score whole plot, including edges.
- Score % crop standing (0-5), leaning (5-45) and % crop lodged (45-90) and crop lodged flat.
- Continue to score lodging at weekly intervals afterwards or after a rain or windy event.

Failure mechanism :

- As soon as possible after lodging, ascertain the point of failure on the plant i.e. stem or anchorage or brackling.
- Record wind speed and direction and rainfall at nearest time to lodging from meteorological station.

Sampling :

- Immediately after lodging, randomly sample ten lodged plants and ten standing plants (if possible) from each lodged plot.
- Measure soil shear strength at each grab sample point. (10 times at 2.5cm depth, 10 times at 5.0 cm depth) Use 19mm shear vane.

Analysis :

- If possible measure natural frequency in lodged plot.
- Measure soil moisture (gravimetric method) using soil collected with shear vane.
- Measure tiller number crop height, ear area and centre of gravity.
- Measure, stem diameter, wall width and if possible stem breaking strength.
- Measure crown root number, rigid length, crown depth and width.

APPENDIX 5

RESIDUAL DEGREES OF FREEDOM FOR EACH SAMPLING DATE

MT95 Sampling dates

GROWTH STAGE	EARLY SOWING	LATE SOWING	Plots sampled	Residual df
GS 30	23/2/95	3/4/95	24	8
GS 31	22/3/95	10/4/95	24	8
GS 33	27/4/95	3/5/95	48	24
GS 39	12/5/95	18/5	48	24
GS 59	5/6/95	5/6/95	6	2
GS 69	26/6/95	26/6/95	96	56
GS 72	3/7/95	3/7/95	6	2
GS 90 (HARVEST)	9/8/95	9/8/95	96	56

MT96 Sampling dates

GROWTH STAGE	EARLY SOWING	LATE SOWING	Plots sampled	Residual df
GS 21 - 27	11/12/95	-	12	4
GS 21 - 27	15/1/96	15/1/96	24	8
GS 21 - 27	14/2/96	14/2/96	24	8
GS 22 - 26	-	18/3/96	24	8
GS 30	18/3/96	22/4/96	24	8
GS 31	2/4/96	29/4/96	24	8
GS 33	26/4/96	14/5/96	48	24
GS 39	24/5/96	31/5/96	48	24
GS 72	1/7/96	4/7/96	96	56
GS 85	31/7/96	31/7/96	24	8
GS 90 (HARVEST)	19/8/96	19/8/96	96	24